

COMPARATIVE ENERGETICS OF CAVIOMORPH RODENTS

BY

ALEXIS ARENDS

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1985

ACKNOWLEDGMENTS

I would like to thank the members of my committee for their encouragement and advice: Dr. John F. Anderson, Dr. Frank G. Nordlie, Dr. Martha L. Crump, Dr. John F. Gerber. I particularly would like to thank my chairman, Dr. Brian K. McNab, who provided intellectual guidance, made my graduate experience a very rewarding one and placed at my disposal resources and facilities in his laboratory which made this project possible.

Part of the research was done at the Centro de Investigaciones en Ecologia y Zonas Aridas of the Universidad Nacional Experimental Francisco de Miranda and I would like to express my gratitude to its authorities for their generous support and encouragement.

Research animals were provided through the kind cooperation of Dr. J. Eisenberg (National Zoological Park, Washington) and Dr. J. Brown (Santa Fe Community College Teaching Zoo, Gainesville, Florida). To them I extend my sincere thanks.

I am grateful to Drs. Ken Prestwich, J. Perran Ross and Hugh Ellis who provided friendship, advice and technical help at early stages of this project. I am also indebted to

Dr. Michel Genoud for many hours of stimulating and critical discussion in which many of these ideas nurtured.

This dissertation profitted from B.K. McNab, J. Eisenberg, M. Roberts and S. Thompson who permitted me to use some of their unpublished observations, for which I am thankful.

I wish to acknowledge the excellent cooperation of W.L. Adams who drew the figures of this paper. Likewise the expertise and invaluable assistance during the preparation of the manuscript of Mrs. Katherine B. Williams of Professional Typing.

I thank Drs. B.K. McNab, F.G. Nordlie and M. Genoud for constructively criticizing this manuscript. They made many useful suggestions and helped in translating it to proper English.

My graduate studies were supported by a scholarship from the Universidad Central de Venezuela.

Many people made my stay in Gainesville pleasant and rewarding and to them I am grateful. I would especially like to express my appreciation to Sachito and Horst Schwassmann, to Greta and Brian McNab and to Esther and Frank Nordlie for sharing their culture and friendship with my family and me.

Finally, I would like to thank my family. I thank my parents for their example and constant encouragement and support. I thank my sons: Tulio Francisco for his spiritual support, and Alberto Jose for being there. Above

all, my deepest gratitude to my wife Miriam whose love, encouragement and untiring support strengthened my resolve at critical times. Without her, I would never have finished.

TABLE OF CONTENTS

	<u>Page</u>
ACKNOWLEDGEMENTS	ii
ABSTRACT	vi
INTRODUCTION	1
THEORETICAL CONSIDERATIONS	5
MATERIALS AND METHODS	10
RESULTS	14
DISCUSSION	46
Standard Rate of Metabolism	46
Thermal Conductance	58
Body Temperature	63
On the Proposed Correlation of Reproduction with Energetics	66
REFERENCES	78
BIOGRAPHICAL SKETCH	88

Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

COMPARATIVE ENERGETICS OF CAVIOMORPH RODENTS

By

Alexis Arends

May, 1985

Chairman: B. K. McNab
Major Department: Zoology

The energetics of eleven species of caviomorph rodents are examined and compared with available information to explore how adaptation to different environmental conditions are reflected on physiological functions, especially energy expenditure.

Standard metabolic rate (SMR) is not a conservative feature of the infraorder Caviomorpha. Most caviomorphs have intermediate to low SMRs. The influence of body size on SMR of caviomorphs is described by the Kleiber relationship. Seventy percent of variation in SMR within the infraorder is explained by the change in body mass. Much of the residual variation is correlated with food habits, substrate adaptation and climate.

Arboreal folivores are characterized by low SMR. In frugivores, the alternate food eaten during periods of low fruit availability seems to determine the level of SMR.

Leaf- and stem-eaters have low standard rates, while nut-eaters have high SMRs.

Caviomorphs that live in xeric environments show a reduction in SMR. Fossorial species have low to intermediate rates, while semi-aquatic forms may have SMRs related to water temperature.

Within the infraorder 87% of the variation in minimal thermal conductance (C_m) is explained by the change in body mass. But large caviomorphs (over 5 Kg) have C_m independent of body size. Caviomorphs adjust to climate mainly through changes in C_m . Tropical caviomorphs have intermediate to very high C_m , while temperate ones have intermediate to low C_m .

As a consequence of the balance between SMR and C_m , tropical and xeric-adapted caviomorphs have temperature differentials with the environment smaller than expected and furthermore that are independent of body size.

Caviomorph rodents are good thermoregulators. The body temperature (T_b) averages 37.0 ± 0.23 , is independent of body size and does not seem to be adaptive to climate. Much of the variation in T_b is correlated with variation in SMR that is independent of size. The interaction of SMR with the reproductive parameters within the infraorder support, in part, the McNab hypothesis of positive correlation between SMR and the maximal intrinsic rate of natural increase of the population (r_m).

INTRODUCTION

The new world hystricognaths (Infraorder Caviomorpha) are the oldest group of rodents in South America. They are known from fossil records of Deseadan age (early Oligocene) 35 million years ago (Woods, 1982). The caviomorphs form part of the second stratum of land mammal fauna of South America (Simpson, 1980). Their origin and relationship has been the center of a long and lively discussion that is still unsettled (Landry, 1957; Hershkovitz, 1972; Patterson and Pascual, 1972; Lavocat, 1974, 1980; Wood, 1974, 1980; Simpson, 1980; for an excellent review see Woods, 1982). Africa, by way of rafting across the Atlantic, and North America, through island hopping, have been proposed as a source of the initial propagule. New evidence suggests the possibility that two different stocks are involved (Bugge, 1974; Sarich and Cronin, 1980; Woods, 1982). One gave rise to the Octodontoidea and the other to the Caviioidea, Erethizontoidea and Chinchilloidea (Sarich and Cronin, 1980; Woods, 1982). Nevertheless, the most accepted view is that rodents of the suborder Hystricognathi are monophyletic (Landry, 1957; Lavocat, 1974; Luckett, 1980; McKenna, 1980; Wood, 1980; Woods, 1982; Carleton, 1984).

Whatever their origin, caviomorph rodents evolved in isolation in South America for at least 30 million years (Webb and Marshall, 1982). By Deseado time they already showed diversification leading toward the four main lineages, with representatives of at least 7 families (Simpson, 1980). Living New World hystricognaths are classified into 4 superfamilies, 13 families, and into approximately 44 genera (Carleton, 1984; Woods, 1982, 1984). They have diversified more than any other similar group of mammals (Hershkovitz, 1972), occupying all the available habitats from cold temperate environments to warm humid tropics, and from semiaquatic to arboreal, as well as fossorial, habits. They range in size from small rat-like echimyids to the large boar-like capybara, and with food habits ranging from grazers and folivores to frugivores and seed-eaters.

Despite these pronounced degrees of ecological divergence, all the forms can be derived from pastoral, terrestrial ancestors (Hershkovitz, 1972). The first South American rodents were small rat-like animals (Simpson, 1980). The great diversity of living species make the caviomorphs an appropriate subject for a study examining how adaptations to different environmental conditions or to different niches are reflected in physiological functions, especially energy expenditure.

Body mass is the most important factor determining energy expenditure (Kleiber, 1947, 1961; Hemmingsen, 1960;

McNab, 1970, 1974, 1983a). Thus the range of body size of caviomorphs (ca. 300-fold) suggests that there may be an appreciable variation in energetics in these rodents; furthermore, it makes them especially suitable for this study in light of the conclusion that, to be able to study the effect of body size on energetics, it is necessary to work with species that have at least a 10-fold difference in body mass (Kleiber, 1947). Because the relationship between size and basal metabolic expenditures is a power function, endotherms at the extremes of body size have greater influences on the relationship than intermediate-sized ones.

In his review of temperature regulation of rodents, Hart (1971) reported that they fit the general relation between metabolism and body size described by Kleiber (1947) and that they also fit the relation between thermal conductance and body size described by Morrison and Ryser (1951) and extended by Herreid and Kessel (1967). In that review only two of the species used were caviomorphs, only one was larger than 5 kg and none was from a tropical climate.

This study proposes, first, to evaluate the effects of body size, climate, food preferences, habits, and phylogeny on the energy expenditure in the infraorder Caviomorpha, and second, to estimate the significance of these parameters by comparing them with other ecological equivalent mammals in light of the suggestion that the level and stability of body temperature in endotherms is determined by

rate of metabolism, insulation, and body size (McNab, 1969, 1970). Furthermore, these parameters, in turn, have been suggested to interact with each other (McNab, 1970), with climatic conditions (Scholander et al., 1950a; McNab and Morrison, 1963; McNab, 1966, 1970, 1973, 1974) and with food habits (McNab, 1969, 1974, 1978a, 1978b, 1983b), so the influence of these factors will also be examined in Caviomorpha as well.

THEORETICAL CONSIDERATIONS

The energetics of temperature regulation in endotherms can be expressed in a simplified form using the model proposed by Burton (1934) and Scholander et al. (1950b). It recognizes the endotherm as a heat machine capable of maintaining a constant body temperature in a changing environmental temperature by adjusting its insulation and its metabolism so that the heat produced is balanced by the rate of heat loss:

$$\dot{V}_{O_2} = C' (T_b - T_a) + L\dot{E} \quad (1)$$

where $\dot{V}_{O_2}$ is rate of oxygen consumption, an indirect measurement of the heat produced by metabolism, C' dry thermal conductance or coefficient of heat transfer (Burton, 1934), which is the inverse of insulation and indicates how easily heat is exchanged between the body and the environment (Burton, 1934; McNab, 1980). T_b is body temperature, T_a ambient temperature, L latent heat of vaporization and $\dot{E}$ the rate of water lost via evaporation.

The term $L\dot{E}$ estimates the evaporative heat loss and at low to moderate ambient temperature it is a small fraction

of the total heat loss. Therefore at these conditions equation (1) becomes

$$\dot{V}_{O_2} = C (T_b - T_a), \quad (2)$$

where C is the "wet" thermal conductance (McNab, 1974). A consequence of equation (2) is that there is zero heat produced at zero temperature gradient (Scholander et al., 1950b), because C is never zero (McNab, 1980c); under this condition T_a must equal T_b .

Adjustment of the energy balance should be achieved at the lowest energy cost (Chatonnet, 1983). Therefore, the model assumes that an endotherm responds to changes in environmental temperature in a sequential and logical order, describing two sets of ambient temperatures. Heat loss is proportional to the temperature gradient between the animal and the environment, then when the external temperature falls, the least expensive way of maintaining body temperature is by decreasing thermal conductance alone (i.e., changes in radiative, conductive, convective and evaporative properties of the animal).

This behavior defines the region of physical thermoregulation (zone of thermoneutrality) in which the metabolism is constant at a minimal, basal (standard) level ($\dot{V}_{bO_2}$). At the lower limit of thermoneutrality (T_1) the thermal conductance theoretically reaches its minimum

(C_m) and the dimensions of the corresponding temperature gradient [$\Delta T_1 = (T_b - T_1)$] describe the capability of the animal for rapid change in overall insulation (Hart, 1957). With further decrease in ambient temperature, the body temperature could only be maintained by the increase in heat production, because C_m is constant (zone of metabolic or chemical heat regulation).

At the lower limit of thermoneutrality equation (2) becomes

$$\dot{V}_{\text{bo}_2} = C_m (T_b - T_1), \quad (3)$$

which allows different species to be compared. Endotherms, within a fixed body size, have then three parameters to affect thermoregulation: $\dot{V}_{\text{bo}_2}$, C_m and ΔT_1 . Any two of these factors can be modified (in an ecological and evolutionary sense), thus setting the third. Usually endotherms modify $\dot{V}_{\text{bo}_2}$ and C_m (McNab, 1969, 1970, 1974), thus determining ΔT_1 .

Both metabolic rate and conductance are mass-dependent functions. Kleiber (1961) showed metabolic rate (MR) of mammals to have the following relationship

$$\text{MR} = 70 \cdot M^{0.75}, \quad (4)$$

where MR is in K cal/day and M in Kg. Equation (4) can be modified (McNab, 1974) to:

$$\dot{V}_{\text{bO}_2}/M = 3.42 M^{-0.25}, \quad (5)$$

where $\dot{V}_{\text{bO}_2}/M$ is in $\text{cm}^3\text{O}_2/\text{g}\cdot\text{h}$, assuming $4.8 \text{ cal}/\text{cm}^3\text{O}_2$ and where M is in g.

Minimal thermal conductance in mammals is related to mass (McNab and Morrison, 1963; Herreid and Kessel, 1967) as:

$$C_m/M = 1.0 M^{-0.50}, \quad (6)$$

where C_m/M is in $\text{cm}^3\text{O}_2/\text{g}\cdot\text{h}\cdot^\circ\text{C}$. ΔT_1 , as a consequence, is also related to body mass.

$$\Delta T_1 = \dot{V}_{\text{bO}_2}/C_m = 3.42 M^{+0.25} \quad (7)$$

Equations (5) and (6) are generalizations used to predict the expected $\dot{V}_{\text{bO}_2}$ and C_m of a "standard" mammal of a given body mass. If an animal shows deviations from these expected values, ΔT_1 will also deviate. Therefore, to account for this deviation equation (7) becomes

$$\Delta T_1 = 3.42 F M^{0.25}, \quad (8)$$

where F is a factor describing the variation of the ratio $\dot{V}_{\text{bo}_2}/C_m$ independent of mass (McNab, 1974). In other words

$$F = f_m/f_c,$$

where f_m is percent of the expected $\dot{V}_{\text{bo}_2}$ and f_c percent of the expected C_m .

MATERIALS AND METHODS

Eleven species of caviomorph rodents were used in this study. Two chozchoris (Octodontomys gliroides), four degus (Octodon degus), two punare (Trichomys apereoides), two green acouchi (Myoprocta acouchy), two rock caviés (Kerodon rupestris), and one chacoan cavy (Dolichotis salinicola) were borrowed from the United States National Zoological Park (Washington, D.C.). Two Azara's agoutis (Dasyprocta azarae paraguayensis) were obtained on loan from the Santa Fe Community College Teaching Zoo (Gainesville, Fla.). Four Chinchilla laniger used were pets donated by University of Florida students for this study. All these animals were born in captivity and were housed at least two weeks before the experiments at the Department of Zoology, University of Florida.

The paca (Agouti paca) was purchased from a private source who raised it as a pet after trapping it near Cabure, Falcon, Venezuela. The reddish agouti (Dasyprocta leporina flavescens) was trapped at El Hatillo, Miranda, Venezuela and was kept in captivity for at least a month before the experiments. The capybara (Hydrochaeris hydrochaeris) was caught in the western llanos of Venezuela and raised in captivity. The paca, reddish agouti, and capybara were

studied at the Universidad Nacional Experimental Francisco de Miranda, Coro, Venezuela.

The animals at both study sites were housed in large indoor cages appropriate for their size. Trays filled with sand were provided to allow the animals to keep their fur in good condition. The temperature of the rooms was maintained between 25 and 28°C and the animals were maintained under a natural diel regime. Water and a varied herbivorous diet were available ad libitum. Most animals maintained or increased their mass, except a female green acouchi that died (from an unknown cause) two weeks after arriving at Gainesville.

Rates of oxygen consumption at various ambient temperatures were measured in an open system employing either an F₃ or G₂ Beckman paramagnetic oxygen analyzer, or a S-3A Applied Electrochemistry oxygen analyzer. Depending upon body size animals were placed either in a 3 l. clear plexiglass chamber, in a 44 l. metal chamber, or in a 329 l. chamber that had double walls through which water from a temperature-controlled water bath was circulated. The outer wall was covered with styrofoam to improve thermal stability inside the chamber. A replicate of this chamber was made in Venezuela for the part of the study performed there. Both the small and medium size chambers were submerged in the water bath to insure that the animals were exposed to a constant predetermined ambient temperature.

Ambient temperature was monitored either with a mercury thermometer ($\pm 0.2^{\circ}\text{C}$) or with a Yellow Springs Instruments (YSI) telethermometer ($\pm 0.1^{\circ}\text{C}$) probe taped to the inner side of the chamber top.

The metabolic chamber had two ports: one to allow fresh room air into the chamber and the other connected through tygon tubing to the negative-pressure side of an air pump that pulled air from the chamber. The flow rate through the chamber was adjusted to suit the experimental temperature and size of the animal. The flow rate was regularly monitored and kept constant within 2% during an experiment. Carbon dioxide was removed from the air stream with color indicator soda lime (8-14 mesh) and then water was absorbed by color indicator silica gel (grade H, type IV, 6-16 mesh) before measuring the flow rate with a Brooks precision rotameter. Temperature of the air stream and barometric pressure were regularly monitored.

The rate of metabolism was calculated and corrected to STPD from the following formula derived from Depocas and Hart (1957):

$$\dot{V}\text{O}_2/M \text{ (c}_m^3\text{O}_2/\text{gh}) = 27.257(\Delta\text{PO}_2 \cdot F_r \cdot P_b) / T \cdot M,$$

where ΔPO_2 is the fractional change in oxygen content in the air stream between the entrance to and exit from the chamber, F_r flow rate (cm^3/min), P_b barometric pressure (mm Hg),

T absolute temperature of the air stream at the site of flow rate measurement ($^{\circ}\text{K}$), and M body mass (g).

The animals were fasted 12 h before the measurements and considered post-absorptive. They were weighed before and after each experiment. All metabolic rates were measured during the quiescent period of the animal (i.e. during daylight hours for nocturnal species and during night for diurnal species). Each run lasted between 2 and 6 h and was terminated when a stable low repeated reading in oxygen consumption maintained for at least 10 min was obtained. Deep rectal temperature was measured before and immediately after each experiment with a YSI telethermometer that was calibrated in a constant temperature water bath with a mercury thermometer ($\pm 0.1^{\circ}\text{C}$).

Standard rates of metabolism (basal) were calculated as the average oxygen consumption within the thermoneutral zone. Minimal "wet" thermal conductances were estimated as the mean value of thermal conductances calculated at low to moderate ambient temperature from equation (2) rearranged as

$$C = \dot{V}\text{O}_2 / T_b - T_a,$$

using individual measurements of metabolic rates ($\dot{V}\text{O}_2$) and their corresponding body temperatures (McNab, 1980c).

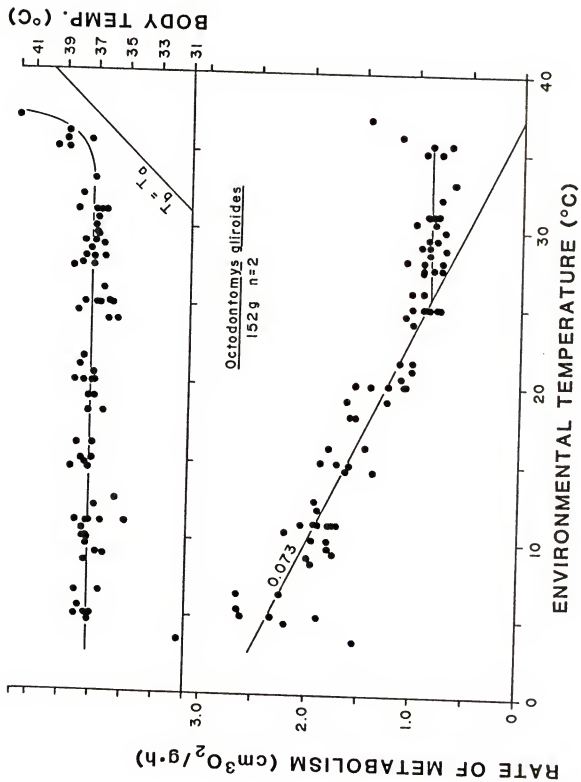
Variation about means was expressed as $\pm$ Standard error, unless otherwise stated.

RESULTS

The relationship between metabolic rate, body temperature, and ambient temperature for the 11 rodent species studied are presented in figures 1 through 11. Parameters extracted from these data are summarized in Table 1 along with data reported in the literature.

The chozchoz, Octodontomys gliroides, is a highland burrowing rodent that is found in arid montane shrub in the Andes between 2,000 and 4,000 m. in Bolivia, Chile, and Argentina. It regulates body temperature at $37.2 \pm 0.08^{\circ}\text{C}$ between ambient temperatures of 4.6 to 34°C (Fig. 1). In the only case studied below 4°C the animal became hypothermic ($T_b = 31.4^{\circ}\text{C}$) after only 1.5 hours. This result was unexpected because of the harsh natural environment faced by this nocturnal species. Correlated with this breakdown in temperature regulation there was a decrease in metabolic rate and in minimal thermal conductance. Octodontomys feeds mainly on leaves, bark, seeds and on cacti fruits (Mann, 1978; Nowak and Paradiso, 1983). They have a low standard metabolic rate (i.e. 88% of expected for an animal of 152 g) and a low minimal thermal conductance (90% of expected), which befits the dense soft fur coat and the climate that these animals face.

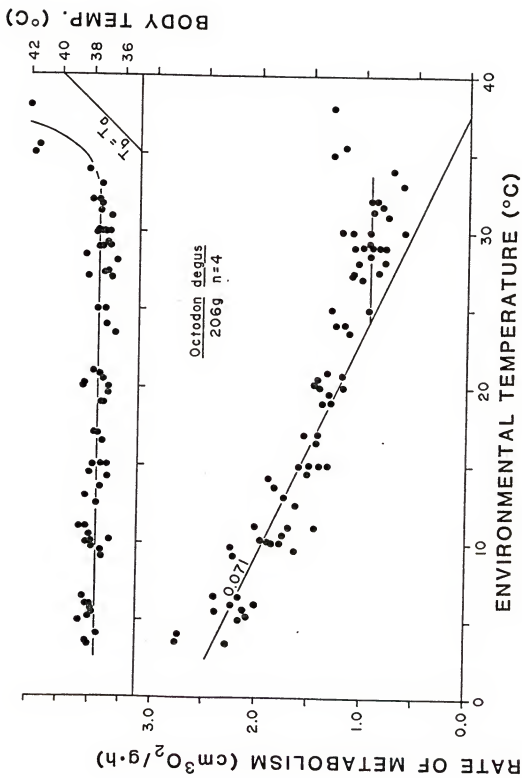
Figure 1. Body temperature and rates of metabolism as a function of environmental temperature in two *Octodontomys gliroides*. Mean standard rates are indicated by the horizontal line in thermoneutrality; mean minimal thermal conductance is indicated both by the absolute value of slope of the curve drawn extrapolated to the mean body temperature at temperatures below thermoneutrality and by the number associated with the curve. The curve for body temperature is fitted by eye.



The degus, Octodon degus, (206 g) is a good thermoregulator, maintaining body temperature ($37.6 \pm 0.06^{\circ}\text{C}$) down to an ambient temperature of 3.4°C (Fig. 2). These stout, diurnal rodents, endemic to Chile, live in semi-arid shrub slopes of the Andes up to 1,200 m (Woods and Boraker, 1975). They are the least fossorial of any of the octodontids. The metabolic rate and thermal conductance are as expected from body mass (103 and 102%, respectively) and are similar to those reported by Rosenmann (1977). Degus store food for winter. They have a broad herbivorous diet, feeding heavily on grasses and seeds (Woods 1984), but during fall and winter concentrate on leaves, stems, conductive tissue and seeds (Woods and Boraker, 1975; Fulk, 1976; Fuentes and LeBoulange, 1977; Meserve, 1981; Simonetti and Montenegro, 1981).

The Punare, Trichomys apereoides, (323 g) is the only echimyid with a distribution limited to areas dominated by rock out-croppings (Streilein, 1982c). They are found within mesic habitats in the semi-arid Caatinga, Cerrado, and rocky areas of the Atlantic rain forest (Mares et al., 1981b; Streilein 1982a, b). They are crepuscular and scansorial (Mares et al., 1981b), feeding on seeds, pods, fruits, grass and cactus pads (Karami et al., 1976, Streilein, 1982a, b). These endemic Brazilian caviomorphs have a low standard metabolic rate (79%) and for a tropical rodent an unexpected low thermal conductance (91% of expected). Unlike most echimyids, Trichomys has a soft and

Figure 2. Body temperature and rates of metabolism in four Octodon degus as a function of environmental temperature. Data analyzed as in Figure 1.



dense fur without spines and a hairy tail (Nowak and Paradiso, 1983). The low thermoconductance compensates for the low metabolic rate and allow punares to maintain body temperature at $37.6 \pm 0.06^{\circ}\text{C}$ (Fig. 3).

The chinchilla, Chinchilla laniger, is bred commercially for its magnificent fur coat that is silky soft and very dense. Chinchillas have as many as 60 hairs growing from each hair follicle (Wilcox, 1950). Not surprisingly, their thermal conductance is low (70%) for a 426 g rodent (Fig. 4). Their natural habitat is the barren areas of the Andes up to 5,000 m where they seek shelter in crevices and holes among rocks (Nowak and Paradiso, 1983). They are known to eat any vegetation available: leaves, seeds, roots and twigs (Zeinert, 1983; Costello, 1965), which is reflected in their low standard metabolic rate (71%).

These results reported in this study (average of 4 females) are lower than the observations of Drozd and Gorecki (1967), who found that minimal resting metabolic rates of 6 male chinchillas were 89% of the value expected of a 403 g animal, and thermal conductance was 94%. Even though we cannot rule out a sex difference, their animals were acclimated to 15°C and were not post-absorptive and the rates obtained were affected by movements of the animals (i.e. were not in basal conditions). Drozd and Gorecki (1967) consider that the standard rate of metabolism was at least 15 to 20% lower than the expected value.

Figure 3. Body temperature and rate of metabolism as a function of environmental temperature in two Trichomys apereoides. Data analyzed as in Figure 1.

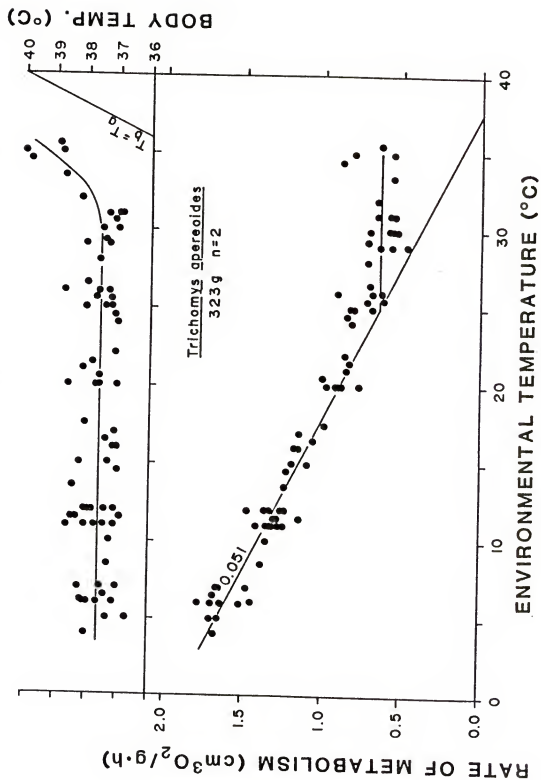
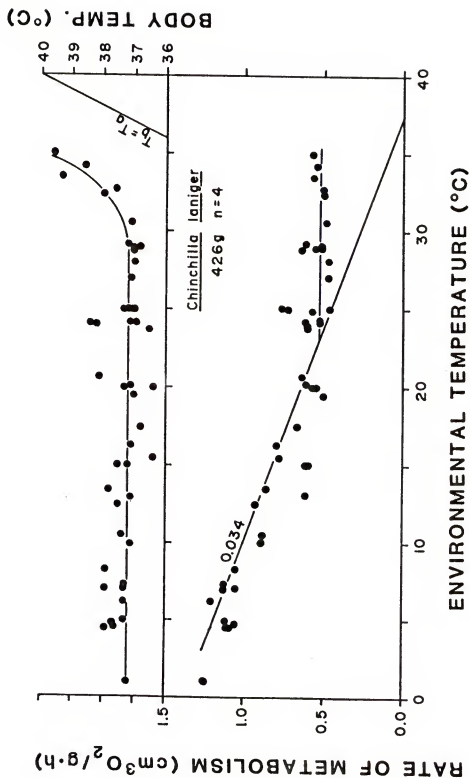


Figure 4. Body temperature and rate of metabolism in four Chinchilla laniger as a function of environmental temperature. Data analyzed as in Figure 1.



Chinchillas are good thermoregulators, maintaining body temperature around $37.2 \pm 0.06^{\circ}\text{C}$ down to ambient temperature of 1°C . Kulzer (1973) in his study of temperature regulation in newborn and infant chinchillas found that they were able to maintain adult levels of body temperatures ($36.6^{\circ}\text{C} \pm 0.5$ S.D.) even when exposed to 0°C . These results conflict with observations of Drozd and Gorecki (1967) who found that chinchillas were somewhat poikilothermic. Body temperatures in their animals varied with ambient temperatures: in the thermoneutral zone it was 35.4°C , but fell to 31.5°C at ambient temperature of 5°C . Verner et al. (1980) reported 24 h-average body temperature of 40.8°C (± 0.35 S.D.) using implanted radio-tele-thermometers. These discrepancies in body temperature may be due to differences in techniques, circadian rhythms or temperature of acclimation, but it also may be differences in fur-keeping by the animals. Chinchillas are known to sandbathe, removing excess lipids from the pelage (Stern and Merari 1969). If sandbathing is prevented, the accumulation of hair lipids mat the pelage, partly exposing skin to the environment (personal observation). So a break-down of thermoregulatory abilities can be expected.

Kerodon rupestris is another caviomorph rodent endemic to Brazil with a distribution limited to rocky areas (Streilein, 1982c). This terrestrial folivore, which lives in dry forest and thorn scrub in the semi-arid Caatinga,

maintains a body temperature around $38.2 \pm 0.07^{\circ}\text{C}$ between ambient temperatures of 3 to 31°C (Fig. 5). It has a low metabolic rate, the level of which seems to be related to the sex and degree of development of the animal.

Lacher (1979), working on growth rates of K. rupestris, reported that animals greater than 500 g were mature. The standard metabolic rate of the sub-adult female (442 g) was 86% of expected and the minimal thermal conductance was 113% while the same female when full-grown (801 g) had a metabolic rate of approximately 70% and a conductance of 120% of expected (McNab, unpublished observation). The young adult male (664 g) had a standard rate 87% and a thermal conductance of 120% of expected.

The Chacoan cavy Dolichotis (= Pediolagus) salinicola (1,613 g) is a good thermoregulator. It maintains a high body temperature ($38.4 \pm 0.03^{\circ}\text{C}$) between ambient temperatures of 5.6° to 35.2°C (Fig. 6). These cursorial rodents are found in arid, thorn-scrub savanna (Mares et al., 1981a), feeding on any available vegetation. Their standard metabolic rate is low (83% of expected) and the thermal conductance, at low ambient temperature, is high (120%). Dolichotis has a higher than expected lower limit of thermoneutrality (27.8°C), because at moderate ambient temperatures its response to a fall in environmental temperature is by a simultaneous change in conductance and in rate of metabolism. There is no clear distinction made in this

Figure 5. Body temperature and rate of metabolism as a function of environmental temperature in two Kerodon rupestris. The dashed curve was obtained on the same female K. rupestris (fully mature) by B.K. McNab (pers. com.). Data analyzed as in Figure 1.

BODY TEMP.(°C)

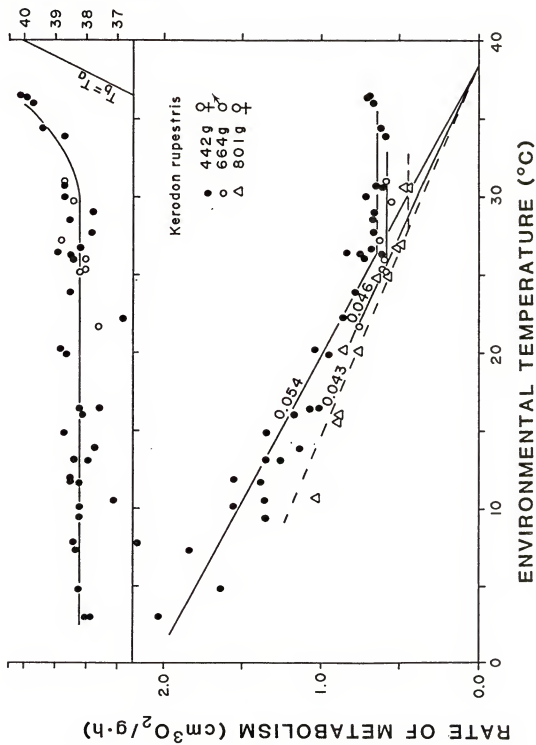
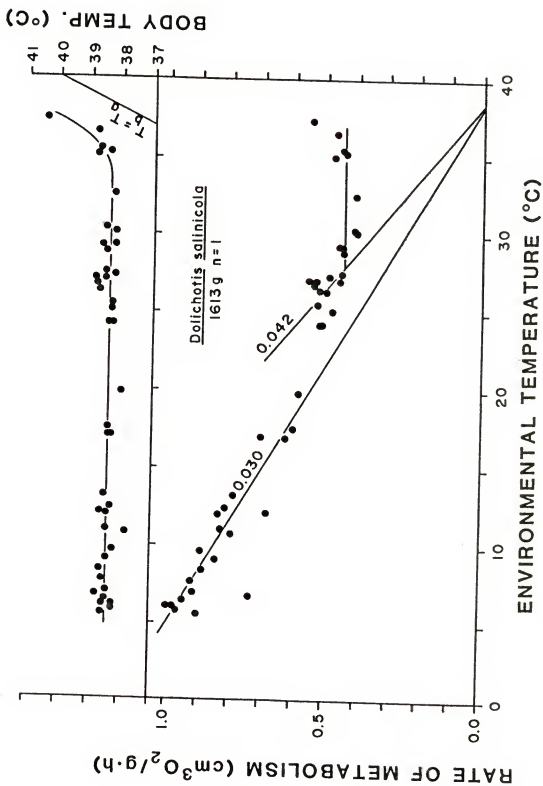


Figure 6. Body temperature and rate of metabolism in one *Dolicholis salinicola* as a function of environmental temperature. Data analyzed as in Figure 1. The lower limit of thermoneutrality is not determined by minimal conductance.



case between the regions of physical and chemical thermo-regulation.

The green acouchi Myoprocta acouchy (= M. pratti) does not conform well with the simplest model of mammalian energetics (Fig. 7). At moderate ambient temperatures it regulates body temperature at $35.4 \pm 0.13^{\circ}\text{C}$ and has a thermal conductance 154% of the value expected for its body mass (914 g). At ambient temperatures below 17°C it maintains a higher body temperature ($37.7 \pm 0.17^{\circ}\text{C}$) and a much higher thermal conductance (186%).

The biology of Myoprocta is poorly known. They are diurnal, cursorial, and live in low-land evergreen tropical forest feeding on fruits and seeds, which they scatter-hoard (Morris, 1962). Their standard rate of metabolism equals 88% of the expected value.

Data on two species of agoutis are presented here: Dasyprocta leporina (= D. agouti) flavescens (2,687 g) (Fig. 8), the reddish agouti of Northern South America and D. azarae paraguayensis (3,849 g) (Fig. 9). The Azara's agoutis has the most southern distribution of all species of agoutis. These cursorial, diurnal, flighty rodents are found in moist tropical forest feeding on large fruits and hard seeds and showing scatter-hoarding behavior. Both Dasyprocta have very high metabolic rates (122% in D. leporina and 113% in D. azarae) and high thermal conductances (159% and 149% of expected respectively).

Figure 7. Body temperature and rate of metabolism as a function of environmental temperature in one Myoprocta acouchy. Data analyzed as in Figure 1.

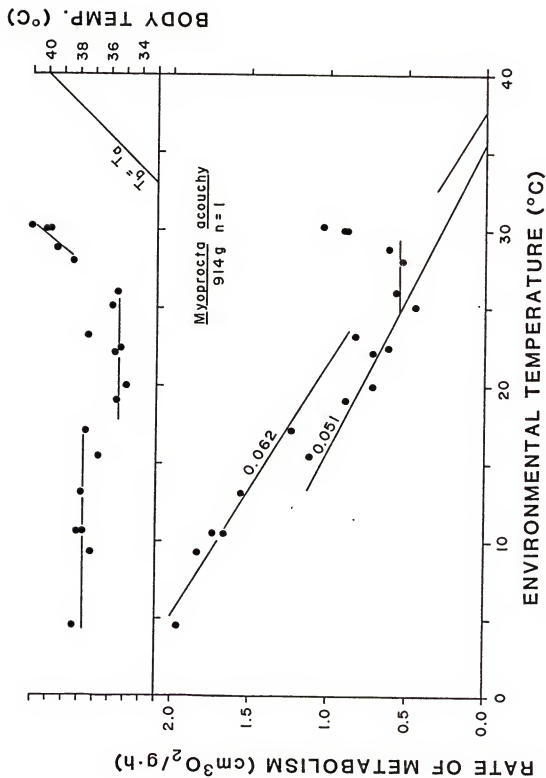


Figure 8. Body temperature and rate of metabolism in one Dasyprocta leporina flavescens
as a function of environmental temperature. Data analyzed as in Figure 1.

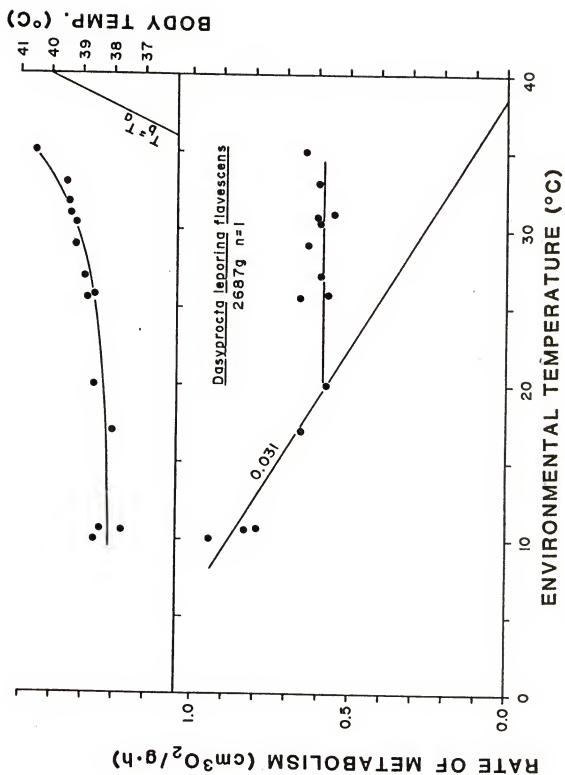
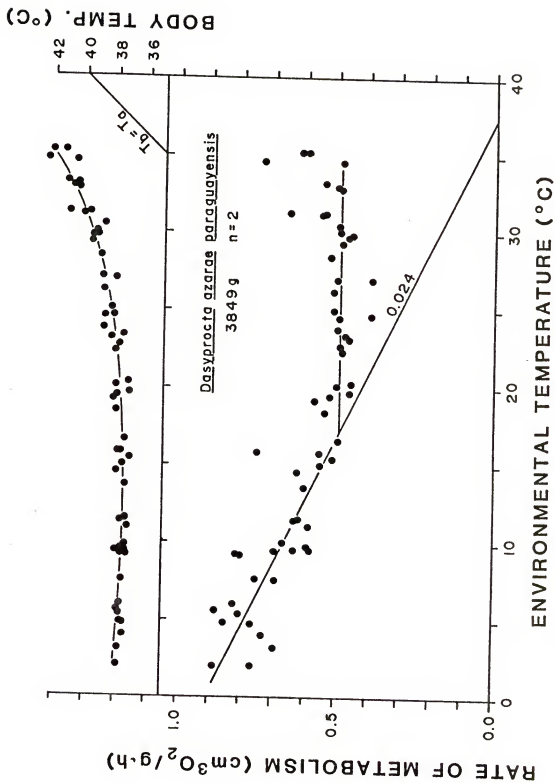


Figure 9. Body temperature and rate of metabolism as a function of environmental temperature in two Dasyprocta azarae paraguayensis. Data analyzed as in Figure 1.



D. azarae is a good thermoregulator (Fig. 9) maintaining body temperature around $37.5 \pm 0.04^{\circ}\text{C}$ at ambient temperatures below the lower limit of thermoneutrality (17.2°C). The few data collected on D. leporina (Fig. 8) suggest it is as precise thermoregulator as D. azarae. Its body temperature fluctuates around 38.3 ± 0.19 . Both Dasyprocta show the interesting behavior of storing heat at ambient temperature greater than 20°C .

The paca, Agouti paca, which also lives in tropical moist forest feeding on fruits and seedlings, does not store heat (Fig. 10), but maintains a body temperature around $37.0 \pm 0.10^{\circ}\text{C}$. Its standard metabolic rate was 105% of the value expected from mass (ca. 4,507 g). McNab (1982) found a metabolic rate of only 86% of expected. This difference may be related to the fact that McNab's paca was fully developed (9,156 g) and very tame, while the one I report here was a young adult (Lander 1974, Matamoros 1980) which constantly tried to escape. The paca has a very high minimal thermal conductance (248%). Similar results were obtained by McNab (1982). These high thermal conductances reflect their large body size and the warm environment in which they live.

Hydrochaeris hydrochaeris the largest living rodent, also has a very high thermal conductance (250% of expected) (Fig. 11), which reflects their coarse and sparse pelage. The semi-aquatic capybara live in savannas and gallery forests surroundings bodies of water and feed on grasses and

Figure 10. Body temperature and rate of metabolism in one Agouti paca as a function of environmental temperature. Data analyzed as in Figure 1.

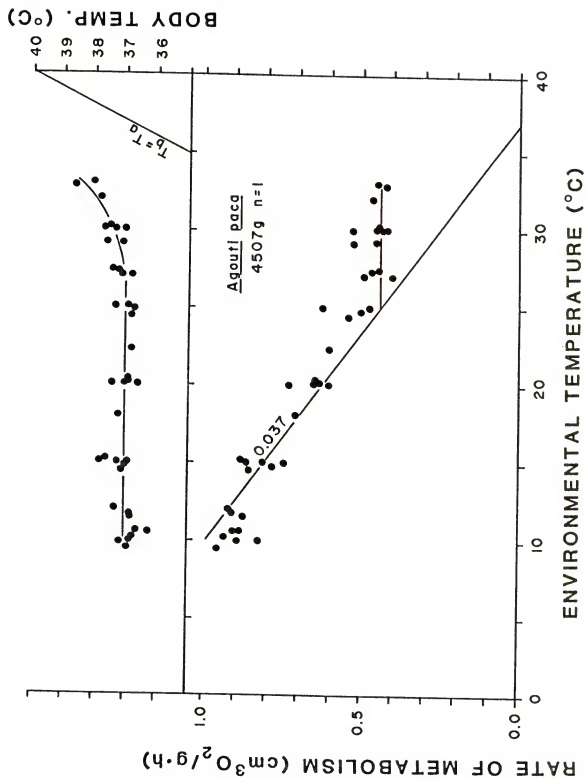
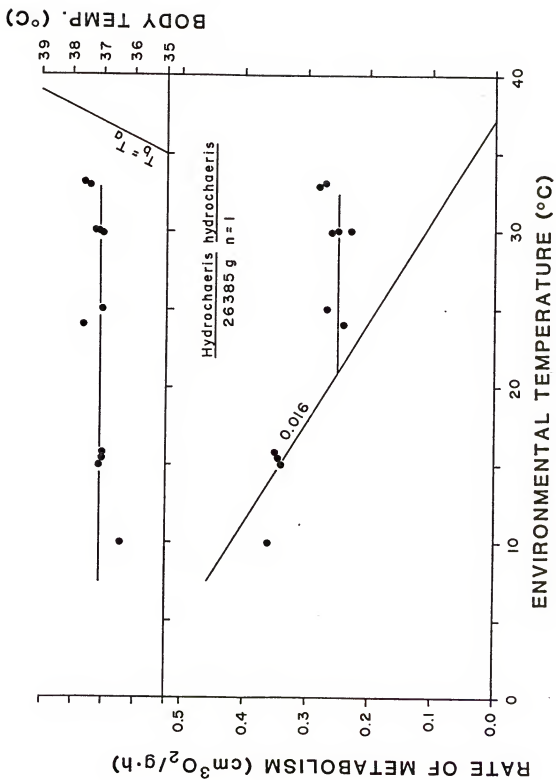


Figure 11. Body temperature and rate of metabolism as a function of environmental temperature in one Hydrochaeris hydrochaeris. Data analyzed as in Figure 1.



aquatic vegetation. They have a standard rate of metabolism that is 93% of expected. The few values reported here were obtained from a young adult male 2 years old, weighing 26.4 Kg. It is possible that fully developed animals will have lower metabolic rates. Hydrochaeris are good thermo-regulators. Body temperature was maintained around $37.1 \pm 0.1^{\circ}\text{C}$. Independent measurements ($n = 150$) of body temperature made in 2 other individuals between 6 a.m. and 9 p.m. (active period) show that when shade and water are available, capybaras maintain body temperature rather precisely ($37.3^{\circ}\text{C} \pm 0.03$) (Arends, unpublished observations).

Table 1. Parameters of Energetics in Caviomorph Rodents.

Species	M (g)	V_{O_2}		n/N	q	$\bar{x} \pm SE$		C _m	n/N	q	F	T _b (°C)	T _h (°C)	ΔT_L	References
		$\bar{x} \pm SE$	$\bar{x} \pm SE$			$\bar{x} \pm SE$	$\bar{x} \pm SE$								
Superfamily Chinchilloidea															
Chinchillidae															
<i>Chinchilla laniger</i>	494	0.47±0.011	17/3	65		0.028		12/3	62		1.05	35.7	25.0	10.2	Kohl (1980)
	426	0.53±0.010	21/4	71		0.034±0.0008		20/4	71		1.01	37.2	21.4	15.7	This study
	403	0.68±0.023	10/6	89		0.047		20/6	94		0.95	35.4	20.0	15.4	Drozdz and
															Gorecki (1967)
<i>Lagostomus maximus</i>	6784	0.28	12/2	74		0.018		2/1	150		0.49	36.8	26.0	11.8	Kohl (1980)
Superfamily Erethizontoidea															
Erethizontidae															
<i>Coendou prehensilis</i>	3280	0.28	12/1	62		0.019		15/1	109		0.57	36.7	26.0	10.7	McNab (1978)
<i>Erethizon dorsatum</i> (ss)	5530	0.43	/2	108		0.014			104		1.04	37.5	6.8	30.7	Irving et al.
(wt)	5853	0.41	/3	105		0.010			77		1.36	37.5	-3.5	41.0	(1955)
	11136	0.25	16/2	76											Roberts M. and S. Thompson (Pers. Com.)
Superfamily Cavioidae															
Caviidae															
<i>Cavia porcellus</i>	629	0.55	30/6	81					42/6	100	0.81	39.0	25.2	13.8	Herrington (1940)
	481	0.58		80											Contreras (1983)
	728	0.55	128/8	84											Kibler et al. (1943)
<i>Dolichotis salinicola</i>	1613	0.45±0.0008	10/1	83		0.030±0.0004		20/1	120		0.69	38.4	27.8	10.6	This study
<i>Kerodon rupestris</i>	442	0.64±0.010	10/1	86		0.054±0.0012		22/1	113		0.77	38.2	26.4	11.8	"
	664	0.59±0.009	6/1	87		0.046±0.0006		3/1	120		0.73	38.2	25.4	12.8	"
	801	0.45±0.005	2/1	70		0.043±0.0012		9/1	120		0.58	38.2	27.7	10.5	McNab, unpublished
<i>Hydrochaeris hydrochaeris</i>	26385	0.25±0.006	5/1	93		0.016±0.0006		4/1	252		0.37	37.1	21.0	16.1	This study
Dasyproctidae															
<i>Dasyprocta leporina flavescens</i>	2687	0.58±0.008	7/1	122		0.031±0.0007		5/1	159		0.78	38.3	19.4	18.9	"
<i>Dasyprocta azarae paraguayensis</i>	3849	0.49±0.007	28/2	113		0.024±0.0004		26/4	150		0.75	37.5	17.2	20.3	"
<i>Myoprocta acouchy</i>	914	0.55±0.035	4/1	88		0.051±0.0019		11/1	154		0.57	35.4	24.7	10.7	"
Agoutidae															
<i>Agouti paca</i>	4507	0.44±0.006	10/1	105		0.037±0.0005		24/1	248		0.42	37.0	25.3	11.9	"
	9156	0.30	/1	86		0.028		/1	268		0.32	37.2	26.0	11.2	McNab (1982)

Superfamily Octodontoidea

Echimyidae

<u>Proechimys semispinosus</u>	498	0.63	8/3	87	0.046	4/3	103	0.85	37.9	24.2	13.7 McNab (1973, 1982)
<u>Trichomys apereoides</u>	265	1.28	8/1	151	0.083	8/1	135	1.12	38.0	24.0	14.0 Schlander et al. (1950a,b)
<u>Capromyidae</u>	323	0.64±0.018	25/2	79	0.051±0.0005	46/2	91	0.87	37.6	25.0	12.6 This study
<u>Corynorhinus pilorides</u>	2630	0.23	14/1	48	0.019	14/1	97	0.49	35.7	24.0	11.7 McNab (1978)
<u>Myocastoridae</u>	4325	0.70	/4	166	0.027	/4	178	0.93	34.6	13.8	20.8 Segal (1978)
<u>Myocastor coypus</u>	206	0.93±0.032	25/4	103	0.071±0.0012	43/4	101	1.02	37.6	24.4	13.2 This study
<u>Octodontidae</u>	195	0.93	/13	102	0.070	39/13	98	1.05	37.2	24.0	13.2 Rosenmann (1977)
<u>Octodontomys gliroides</u>	152	0.86±0.019	30/2	88	0.073±0.0013	44/2	90	0.98	37.2	25.5	11.7 This study
<u>Spalacopus cyanus</u>	83	0.96±0.023	16/8	85	0.088±0.0023	29/8	80	1.06	36.7	26.0	10.7 Contreras (1983)
	136	0.75±0.026	15/9	74	0.074±0.0015	32/9	85	0.87	36.4	26.4	10.0 "
	185	0.79±0.020	19/2	85	0.080±0.0020	21/2	109	0.78	36.4	26.5	9.9 McNab (1979)
<u>Aconaemys fuscus</u>	112	1.08±0.017	13/2	104	0.090±0.0019	18/2	95	1.09	37.3	25.3	12.0 Contreras (1983)
<u>Ctenomyidae</u>	117	0.82±0.018	12/3	78	0.073±0.0016	12/3	82	0.96	36.4	25.3	11.1 "
<u>Ctenomys sp</u>	197	0.66±0.019	8/1	72	0.057±0.017	11/1	81	0.89	36.4	24.7	11.6 "
<u>Ctenomys maulinus</u>	215	0.87±0.019	9/2	98	0.056±0.0017	11/6	82	1.19	36.2	20.7	15.5 "
<u>Ctenomys brunneus</u>	275	0.54±0.037	15/6	76	0.050±0.0074	25/6	81	0.89	35.6	22.7	12.9 "
<u>Ctenomys fulvus</u>	300	0.83±0.015	13/2	78	0.046±0.0013	13/2	79	0.98	36.6	22.9	13.7 "
<u>Ctenomys peruanus</u>	490	0.45	2/	62	0.056	2/	124	0.50	35.2	27.2	8.0 McNab (1979)

M = Body mass, g.

 V_{bo_2} = Standard rate of metabolism, $\text{cm}^3/\text{g.h.}$ $\%V_{\text{bo}_2}$ = Standard rate of metabolism as a percentage of the Kleiber relation, $3.42 M^{-0.25}$. C_m = Minimal thermal conductance, $\text{cm}^3/\text{g.h.}^\circ\text{C.}$ F = $\% V_{\text{bo}_2} / \% C_m$. $\%C_m$ = Minimal thermal conductance as a percentage of $1.00 M^{-0.50}$ (McNab and Morrison 1963). T_b = Body temperature, $^\circ\text{C.}$ T_l = Lower limit of thermoneutrality, $^\circ\text{C.}$ ΔT_l = Temperature differential between T_b and T_l , $^\circ\text{C.}$ n/N = Number of measurements/number of animals.

DISCUSSION

Standard Rate of Metabolism

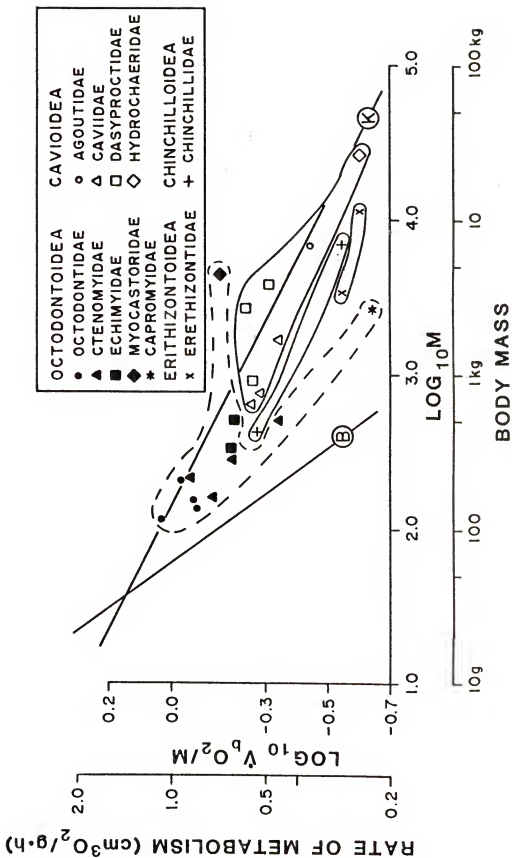
Mass-specific standard rates of metabolism (SMR) in caviomorph rodents are plotted in Fig. 12 as a function of body mass. Most of the species studied (18/24) have intermediate (90-110% of expected) to very low (< 60% of expected) metabolic rates compared to the Kleiber relationship. The two most diverse superfamilies, Octodontoidea and Caviioidea, have representatives with high (111-140% of expected) to very high (> 140% of expected) rates. Such variability indicates that SMR is not a conservative feature of caviomorph rodents.

Body mass is the principal factor influencing the energy expenditures of caviomorphs (Fig. 12), as it is in other endotherms (McNab, 1974). The regression of SMR on body mass in caviomorphs is described by the relationship

$$\text{SMR} = 2.71 M^{-0.24}$$

Neither the exponent nor the constant is significantly different from the Kleiber relationship (F-test, $P > 0.05$; Sokal and Rohlf, 1969). The importance of body size can be shown by the observation that 70% of the variation in SMR is

Figure 12. Mass-specific standard rates of metabolism of caviomorph rodents as a function of body mass. Kleiber (1961) relation is indicated by the linear curve labelled K. The minimal boundary curve for endothermia (McNab, 1983) is labelled B. Data from Table 1. Independent values (in standard conditions) for a particular species were averaged.



explained by the variation in body mass. Much of the residual variation is correlated with food habits, substrate adaptations, and climate.

The effect of food habits on SMR have been extensively studied by McNab (1969, 1973, 1978a, 1978b, 1979a, 1980a, 1980b, 1983b, 1984, 1985). Caviomorphs have food habits that are associated with low rates of metabolism in other mammals (Fig. 13). Specialization on foods with low digestibility, high content of toxic compounds, seasonal unavailability or reduced caloric density because of a mixture with non-nutritive particles, may require a low SMR (McNab, 1980; 1983b, 1985).

Arboreal folivores are characterized by low rates of metabolism. The degree of the depression in SMR is related to the proportion of leaves in the diet (McNab, 1978b). Leaves are one of the most abundant food resources, but are eaten by few vertebrates. Leaves are lower in fiber content but higher in secondary compounds than are grasses (Parra, 1978). Many of these secondary compounds are toxic to mammals (Freeland and Janzen, 1974) and may result in reduced intake to avoid toxic levels, or will reduce the net energy intake because of the cost of detoxification (Freeland and Janzen, 1974; McNab, 1985).

Arboreality, per se, when coupled to large body size (Fig. 14), also leads to low rates of metabolism (Palacio, 1977; McNab, 1978b). This effect seems to be related to the

Figure 13. Mass-specific standard rate of metabolism of caviomorph rodents as a function of body mass as influenced by food habits. Symbols as Figure 12.

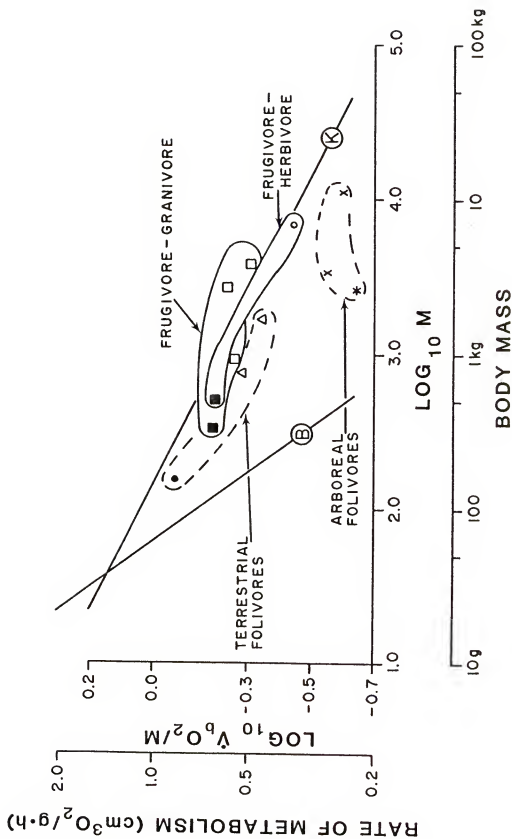
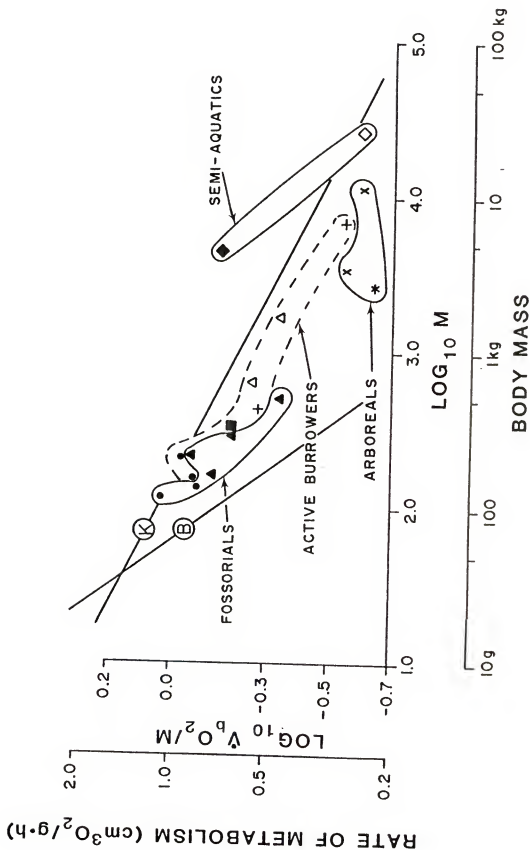


Figure 14. Mass-specific standard rate of metabolism of caviomorph rodents as a function of body mass as influenced by substrate adaptations. Symbols as in Figure 12.



marked reduction of muscle mass in arboreal mammals (Grant, 1978; McNab, 1978b). Thus, the interaction of arboreality with folivory will reduce further the SMR. For example Kerodon, Octodontomys, and Dolichotis are terrestrial folivores and have low SMR but Capromys, Coendu, and Erethizon, arboreal folivores, have low to very low SMRs.

Fruits are a very important food resource in the tropics and their year-round availability is responsible in part for the high diversity of tropical mammals (Fleming, 1973). The different kinds of tropical fruits can be broadly classified into two categories based upon their availability and quality as a food resource.

Soft, small-seeded fruits are rich in carbohydrates and low in proteins (Morton, 1973; Howe and Estabrook, 1977), but they are available throughout the year (Smythe, 1970), whereas large-seeded fruits that are high in lipids and proteins (Snow, 1962; Howe and Estabrook, 1977) tend to be more seasonal. The net result of these patterns is that fruits are relatively scarce in the late rainy season and early dry season (Glanz, 1982; Smythe et al., 1982).

Frugivory is well represented among caviomorph rodents, but the seasonal variation in abundance of fruit has marked effects on their behavior (Smythe, 1970, 1978). During seasonal fruit shortages pacas browse more leaves and fall back on reserves of stored fat, while agoutis live on large seeds that they have buried (Smythe et al., 1982). The

alternative foods that caviomorphs eat during periods of low fruit availability seem to determine the level of SMR.

Leaf- and stem-eaters, like pacas and Proechimys, have low SMRs (Fig. 13). Interestingly enough, pacas and Proechimys prefer soft fruits, as bats do (Glanz, 1982; Emmons, 1982). McNab (1969, 1982) has shown that frugivorous bats have intermediate SMRs if they weigh less than 100 g, but have low SMRs at larger sizes. Seed-eaters, that concentrate on large hard-shelled seeds as do agoutis, have high SMRs. This hard-nut eating guild has been described by Glanz (1982). Agoutis compete for these seeds mainly with squirrels and peccaries (Glanz, 1982) and all have high SMR (McNab, 1985). The low SMR of Myoprocta seems to digress from this pattern. We cannot answer yet whether their low SMR is related to more browsing or perhaps to more active burrowing by the green acouchi than by agoutis. Very little is known on the biology of this species. Myoprocta resembles Dasypsecta but is smaller. In captivity both behave similarly: they scatter-hoard, they sit erect, holding the food in their hands and they also eat hard-shelled seeds. Nevertheless, more information on their natural history is needed.

The low SMR of Trichomys may be related to the semi-arid conditions to which they are adapted. Seed-eaters that feed on small seeds, especially in arid environments, have low SMR, as in the case of heteromyids (McNab, 1979a).

Grazing mammals, such as Octodon, have intermediate to high SMRs (McNab, 1983b, 1985). Cavia and Lagostomus are ecologically equivalent to burrowing sciurids (Hershkovitz, 1972; Mares and Ojeda, 1982), and they likewise have low SMRs regardless of their grazing habits (McNab, 1985).

The influence of climate on the level of SMR is difficult to separate from the effect of food habits. Endotherms living in xeric environments, as Octodontomys, Chinchilla, Kerodon and Trichomys do, show a reduction in SMR (McNab, 1973, 1974; Goyal and Ghosk, 1983), especially if they face problems balancing the water budget (McNab, 1979a) or if they feed on resources that are undependable (McNab, 1979a, 1985). Fossorial and active burrowing mammals also show influences due to the physical environment.

The energetics of fossorial caviomorphs have been studied by McNab (1979b) and Contreras (1983). Fossorial mammals tend to have small body sizes, intermediate to low SMR and intermediate to high minimal thermal conductances, especially when living in constantly warm environments. These characteristics have been interpreted as a means of reducing the probability of overheating when digging or when exposed to high burrow temperatures and also as a means of reducing gas exchange in hypoxic, hypercapnic conditions (McNab, 1979b; Contreras, 1983). Although fossorial caviomorphs are well represented in temperate South America, none live in the tropical moist forest or north of 10° South Latitude (Mares and Ojeda, 1982).

Active burrowing mammals share, in part, the problems of fossoriality and they also have low SMR, especially when coupled to a large body mass (McNab, 1979b, 1980b). This seems to be the case in Lagostomus, Cavia, Chinchilla, Octodontomys, and Dolichotis.

Fossorial mammals exhibit a scaling relation for mass-specific metabolism that is much steeper than is typical of the Kleiber relation. Contreras (1983) has shown that they scale SMR according to the function

$$\text{SMR} = 9.75 \text{ M}^{-0.51},$$

which means that a comparison of SMR to the Kleiber curve does not completely eliminate the influences of body size.

The difference in SMR between Myocastor and Hydrochaeris (Figure 14) may be related to the water temperature in which they live. Aquatic habits present special problems to the animals because of the high rate of heat loss in the water. Aquatic herbivores seem to have high rates of metabolism if they live in cool waters, as in the case of Myocastor, Arvicola, and Ondatra, but intermediate to very low SMRs if they live in warm waters, as to Hydrochaeris, Neofiber and Trichetus. Aquatic carnivores living in cold water have high rates of metabolism, except for the Australian water rat Hydromys chrysogaster which has an intermediate SMR (Dawson and Fanning, 1981). However, H. chrysogaster is tropical in origin and cannot maintain a

constant T_b when exposed to water temperatures below 25°C for extended periods (Dawson and Fanning, 1981). The tropical water opossum Chironectes minimus has a metabolic level higher than that expected for marsupials (McNab, 1978a), but it still is lower than eutherian levels. The case of Ondatra and Neofiber is illustrative. Both are semi-aquatic microtines. McNab (1983b) has shown that small microtines have higher relative SMRs than large ones, but Neofiber which live in warmer waters and are smaller (276 g) than Ondatra (842 g), have relatively lower SMRs (1:01 to 1:29) (See McNab, 1985). Clearly more studies, especially on the large group of semi-aquatic rodents and in the tropical freshwater dolphin Inia, should be made to determine if it is a real pattern or an artifact of the small number of aquatic species studied.

Thermal Conductance

The principal manner by which endotherms adjust to the climate is through thermal conductance (Scholander et al., 1950a). The influence of body size on the minimal thermal conductance of caviomorphs, smaller than 6 kg, is described by the equation

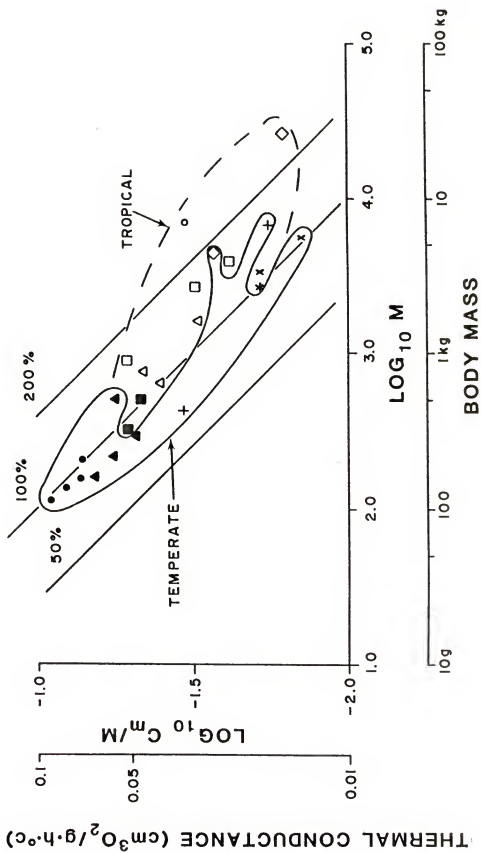
$$C_m/M = 0.47 M^{-0.38}.$$

Eighty-seven percent of the variation in the specific minimal thermal conductance is explained by the variation in

body size. In large caviomorphs C_m seems to be independent of body size (Fig. 15). A similar critical mass (5 kg), in which C_m become independent of body size, was reported by McNab (1976) and by Bradley and Deavers (1980) for mammals in general.

The existence of this critical mass has not been explained. Minimal thermoconductance represents the overall body thermal conductance. It represents the sum of internal and external factors that affecting heat transfer from inside the body to the external environment (Burton, 1934; Scholander, 1950b). Scholander et al. (1950c) and Irving (1951) observed that there is a good correlation between thickness of the fur and its insulative effect and that among arctic mammals, the thickness of the fur increases with size up to that of the arctic fox (i.e. 5 kg) above which it becomes independent of body size. Therefore, the dependence of C_m on mass may be mainly determined by the thermal properties of the fur coat (see also Hart, 1971), but above 5 kg the effect of body size, per se, (i.e. internal factors) predominate. An alternative hypothesis is that because the total heat production shows a greater increase with mass than surface area, 5 kg represents the boundary at which the mammals change emphasis from heat conservation to heat dissipation. Clearly more data on larger species are needed to be able to assess this change in pattern.

Figure 15. Minimal thermal conductance (C_m) as a function of body mass in caviomorph rodents. Data from Table 1. The curve labelled 50, 100 and 200% correspond to percentages of the McNab and Morrison (1963) relation. Symbols as in Figure 12.



The effect of climate on C_m is clearly shown by the comparison between tropical and temperate species. Mammals that live in the lowland tropics typically have higher conductances (Scholander et al., 1950a; McNab, 1969, 1970, 1974; Hart, 1971). In fact, tropical caviomorphs have intermediate to very high C_m while temperate species have intermediate to low C_m (Fig. 15). The high thermal conductances in Lagostomus and in Ctenomys peruanus are related to the coupling of large body size with burrowing habits in seasonally warm environments, while the high thermal conductances of Myocastor undoubtedly is compensatory for the very high SMR of this species.

Endotherms of large body size, since they have higher total heat production and a smaller surface-to-volume ratio, have the potential for overheating increases in warmer environments. It is not surprising then, that many large tropical animals are naked (McNab, 1976). Only two rodents are naked: the naked mole-rat Heterocephalus glaber and the capybara. Heterocephalus is a small (39g) fossorial rodent that lives in semi-desert regions of tropical Africa and faces high burrow temperatures (30.1°C; McNab, 1966). In both species nakedness increases the rate of heat loss to avoid overheating (compare with McNab, 1966). The capybara, besides being naked, uses the water as a heat sink. In fact, they behaviorally thermoregulate shuffling between sun, shade, and water to maintain a very stable body temperature (Arends, unpublished results).

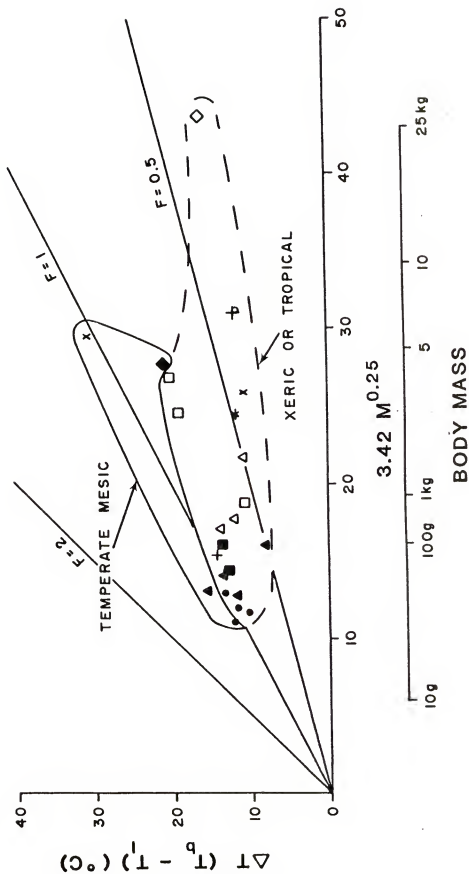
Body Temperature

In endotherms, the interaction between body mass, SMR and C_m defines the temperature differential (ΔT_1) at the lower limit of the thermoneutral zone. This critical gradient (as was defined by Scholander et al., 1950a,b) increases with body mass (see equation 7) and is correlated with climate. Tropical species have smaller ΔT_1 than cold-adapted ones (Scholander, 1950a).

Mesic-temperate caviomorphs, as expected, increase ΔT_1 with body size (Fig. 16), but caviomorphs liveing in xeric or tropic conditions have critical gradients smaller than expected and furthermore independent of body mass as a consequence of the balance between SMR and C_m . Similar independence of ΔT_1 from body size has been shown in heteromyid rodents (McNab, 1979a), and in fossorial and burrowing mammals (McNab, 1979b, 1980b; Contreras, 1983). Interestingly, as reported by McNab (1976) for mammals in general, the greatest ΔT_1 is maintained by species of approximately 5 kg, as a result of the very high C_m of large caviomorphs (Fig. 16).

Caviomorph rodents are good thermoregulators. An analysis of Fig. 12 shows that all of them have SMRs above the boundary curve. McNab (1983a) has postulated that this boundary relationship separates effective endothermia from endothermia with daily torpor (heterothermia). Thus, no caviomorph is known or expected to enter torpor. They

Figure 16. The temperature differential maintained at the lower limit of thermoneutrality as a function of body mass and the factor F in caviomorph rodents. Data from Table 1. Independent values (in standard conditions) of a particular species were averaged. F represents the slope from the linear curves. Symbols as in Figure 12.



maintain an appreciable temperature differential with their environment and resort to behavioral means to reduce the energy expenditure.

The least variable parameter in the energetics of caviomorphs is body temperature (Fig. 17). They have an intermediate T_b that averages $37.0 \pm 0.23^\circ\text{C}$ and that is independent of body size. T_b in caviomorphs is not adapted to climate. A similar conclusion was reported by Scholander et al. (1950a), Irving (1951) and Morrison and Ryser (1952) for mammals in general. However, McNab and Morrison (1963) and Hart (1971) have found that in rodents, warm-climate or desert species have lower T_b than mesic-adapted ones. Furthermore, McNab (1980b) has shown that temperate armadillos and bandicoots have higher T_b than tropical species. The available data for caviomorphs show, if any, the reverse trend.

Much of the variation in body temperature is correlated with variations in SMR independent of the influence of body mass (Fig. 18). Within a family, high T_b is found generally in species with high SMR. High T_b is the result, not the cause, of high SMR (McNab, 1984) and its interaction with the rate of heat loss.

On the Proposed Correlation of Reproduction With Energetics

McNab (1980a) has suggested that one advantage of a high metabolic rate in eutherians is that it augments the maximal intrinsic rate of natural increase of the population

Figure 17. Body temperature as a function of body mass in caviomorph rodents. Independent values for a specie were averaged. Data are from Table 1. Symbols as in Figure 12.

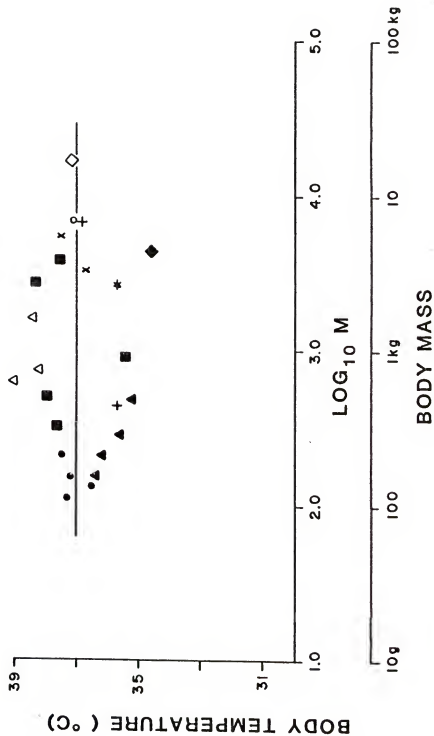
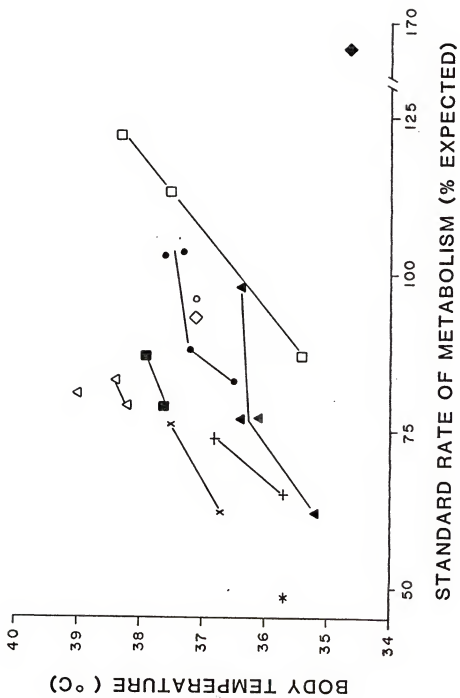


Figure 18. Body temperature in caviomorph rodents as a function of standard rate of metabolism independent of the effect of body mass (fm). Data from Table 1. Symbols as in Figure 12. Species within the same family are connected.



(r_m). This increment in r_m is independent of the effect of body size (Fenchel, 1974) and results from the influence of SMR on gestation period, post-natal growth constant and fecundity (McNab, 1980a). Most recently Hennemann (1983) provided empirical support for this hypothesis of positive correlation between r_m and SMR but, in a re-analysis of his data base Hennemann (1984) points out that species with precocial neonates show weaker correlation between r_m and SMR than species with altricial offspring. Since caviomorphs are precocial and conservative in reproductive features (Weir, 1974; Kleiman et al., 1979; Woods, 1982) it should be of interest to study in them the relationship of SMR with various reproductive parameters.

An increase in r_m , in the evolutionary sense, requires a decrease in the generation time of the population or an increase in fecundity. Generation time is the mean parental age of the population (Pianka, 1978), thus a decrease in gestation time, or an increase in pre-natal or post-natal growth rate will reduce the generation time.

In caviomorphs the scaling of gestation length (days) with body mass (g) is described by the equation:

$$GL = 34.78 M^{0.15}$$

($n = 35$, F-test, $P < 0.01$; Arends, unpublished results). The data available (Fig. 19) for those species in which SMR is known, do not show a significant correlation ($n = 18$, Spearman's rank correlation $r_s = -0.302$, $P > 0.05$) between gestation length (as percentage of the value expected from

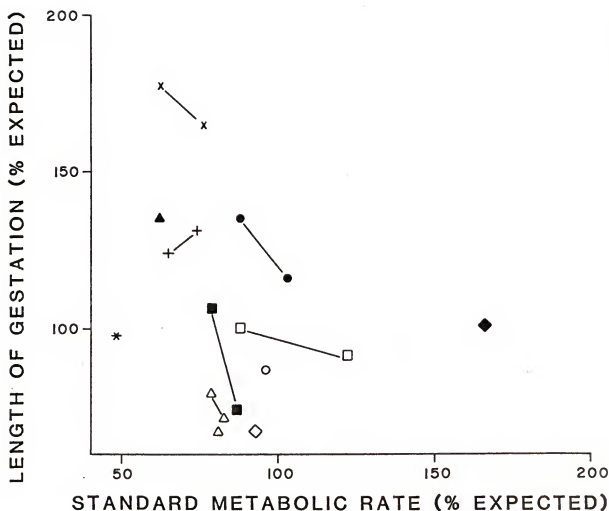


Figure 19. Length of gestation in caviomorph rodents, expressed as a percent of the mass-dependent relation $GL = 34.78 M^{0.15}$ (Arends, unpublished results), as a function of standard rate of metabolism, expressed as a percent of the rate expected from Kleiber's (1961) relation (fm). Symbols as in Figure 12. Species within a family are connected.

body mass) and f_m . Nevertheless, of the six families in which there are data on more than one species, five show the negative trend predicted (McNab, 1980a).

The published data on prenatal growth constant of caviomorphs (Roberts and Perry, 1974) are insufficient to make meaningful comparisons, thus the growth rate at birth (litter mass/gestation length) would be used (Payne and Wheeler, 1968). The relationship between growth rate at birth and maternal body mass in caviomorphs is:

$$\text{GRB (g/days)} = 0.018 M^{0.67}$$

($n = 31$, F-test, $P < 0.01$; Arends, unpublished results). Using this equation to correct for body size results in a positive correlation ($n = 17$, $r_s = 0.484$, $P < 0.05$) between growth rate at birth (percentage of expected) and f_m (Fig. 20). Since gestation length is independent of metabolic rate, an increase in SMR means that total litter mass should increase, which implies that the number of offspring or their size increases.

Recently Zullinger et al. (1984) reported that the postnatal growth of mammals was best described by the Gompertz model. The regression of the Gompertz growth constant on adult body size of 331 species gave the following relationship:

$$K = 0.126 M^{-0.302}$$

which permits a correction for the influence of body size on this parameter. The post-natal growth constant of

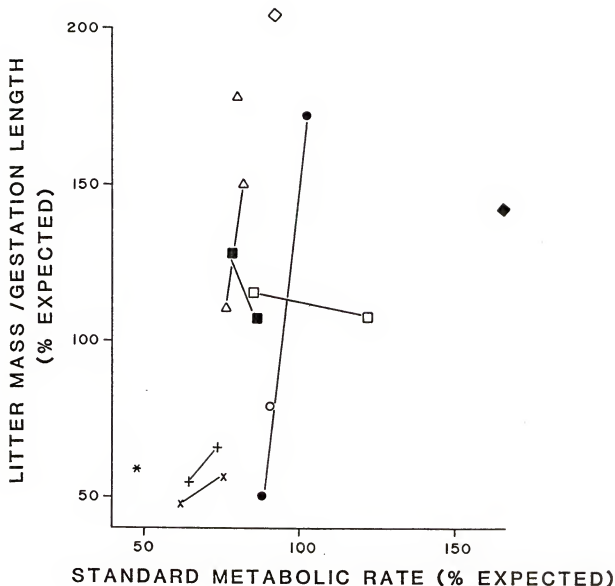


Figure 20. Growth rate at birth of caviomorph rodents, expressed as a percent of the mass-dependent relation $GRB = 0.018 M^{0.67}$ (Arends, unpublished results), as a function of Standard metabolic rate, expressed as a percent of the rate expected from Kleiber's (1961) relation (fm). Symbols as Figure 12. Species within a family are connected.

caviomorphs (Fig. 21) does not appear to be sensitive to changes in f_m ($n = 9$, $r_s = 0.383$, $P > 0.05$).

The fecundity in caviomorphs can be estimated, as annual productivity, assuming that there is a fertile post-partum estrous, such that the interbirth interval is equal to gestation time. This assumption is reasonable especially in small-sized caviomorphs because a great number of species do show a post-partum estrous (Weir, 1974) and the time period of one year reduces the error made in larger species because they have longer gestation periods. The regression of annual productivity on body size is described by the equation:

$$N \text{ Young} / \text{♀} \cdot \text{Year} = 48.6 M^{-0.27}$$

($n = 35$, F-test, $P < 0.01$; Arends, unpublished results). Annual productivity independent of size is positively correlated with f_m ($n = 18$, $r_s = 0.464$, $P < 0.05$) (Fig. 22). Furthermore all six families show the same positive trend.

These analyses of the interaction of SMR with the reproductive parameters of caviomorphs lead to the conclusion that within the infraorder an increase in SMR influences r_m mainly through an increase in fecundity, supporting in part the hypothesis proposed by McNab (1980a).

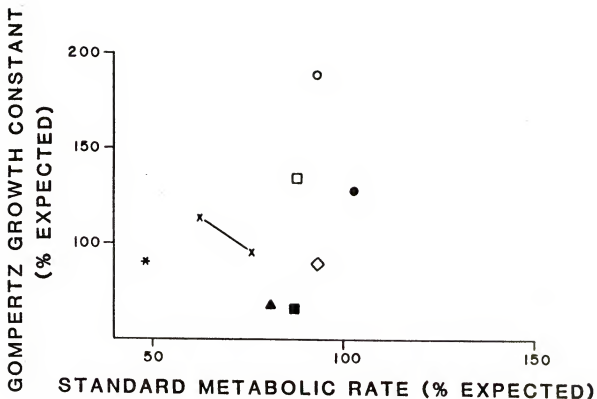


Figure 21. Gompertz growth constant of caviomorph rodents, expressed as a percent of the mass-dependent relation of Zullinger et al. (1984), as a function of Standard metabolic rate, expressed as a percent of the rate expected from Kleiber's (1961) relation (fm). Symbols as Figure 12. Species within a family are connected.

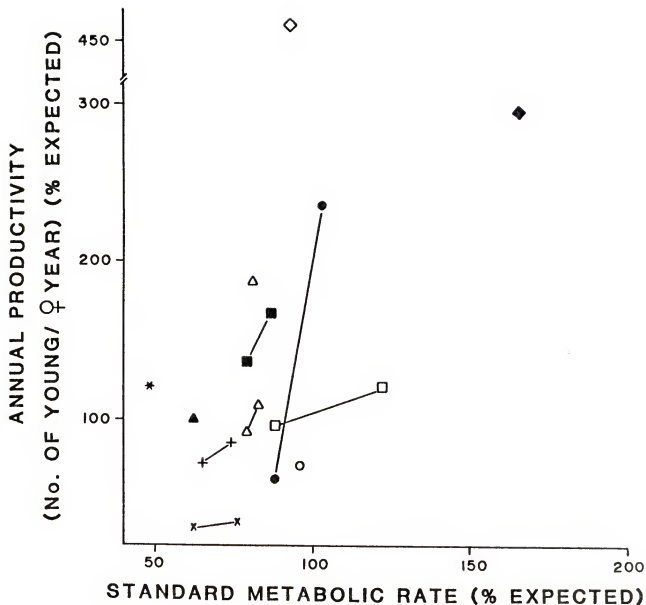


Figure 22. Annual productivity of caviomorph rodents, expressed as a percentage of the mass-dependent relation $P = 48.6 M^{-0.27}$ (Arends, unpublished results), as a function of Standard metabolic rate, expressed as a percent of the rate expected from Kleiber's (1961) relation (fm). Symbols as Figure 12. Species within a family are connected.

REFERENCES

- Bradley, S.R., and D.R. Deavers. 1980. A reexamination of the relationship between thermal conductance and body weight in mammals. *Comparative Biochemistry and Physiology* 65A:465-476.
- Brody, S. 1945. *Bioenergetics and growth*. Reinhold Publishing Corp, New York, New York, USA.
- Bugge, J. 1974. The cephalic arteries of Hystricomorph rodents. In I.W. Rowlands and B. Weir, editors. *The Biology of Hystricomorph Rodents*. Academic Press, New York, New York, USA.
- Burton, A.C. 1934. The application of the theory of best flow to the study of energy metabolism. *Journal of Nutrition* 7:497-533.
- Carleton, M.D. 1984. Introduction to Rodents, In S. Anderson and J.K. Jones, Jr., editors. *Orders and Families of Recent Mammals of the World*. J. Wiley and Son, Inc, New York, New York, USA.
- Chatonnet, J. 1983. Some general characteristics of temperature regulation. *Journal of Thermal Biology* 8:33-36.
- Contreras, L.C. 1983. *Physiological ecology of fossorial mammals: A comparative study*. Dissertation. University of Florida, Gainesville, Florida, USA.
- Costello, H.H. 1965. A primer on chinchillas. *Modern Veterinary Practice* 46:194-198.
- Dawson, T.J., and F.D. Fanning. 1981. Thermal and energetic problems of semiaquatic mammals: A study of the Australian water rate, including comparisons with the platypus. *Physiological Zoology* 54:285-296.
- Depocas, F., and J.S. Hart. 1957. Use of the Pauling oxygen analyser for measurement of oxygen consumption of animals in open-circuit systems and in a short-lag, closed-circuit apparatus. *Journal of Applied Physiology* 10:388-392.

- Drozdz, A., and A. Gorecki. 1967. Oxygen consumption and heat production in chinchillas. *Acta Theriologica* 12:81-86.
- Emmons, L.H. 1982. Ecology of *Proechimys* (Rodentia, Echimyidae) in south-eastern Peru. *Tropical Ecology* 23:280-290.
- Fenchel, T. 1974. Intrinsic rate of natural increase: The relationship with body size. *Oecologia* (Berlin) 14:317-326.
- Fleming, T.H. 1973. Numbers of mammals species in North and Central American forest communities. *Ecology* 54:555-563.
- Freeland, W.J., and D.H. Janzen. 1974. Strategies in herbivory by mammals: The role of plant secondary compounds. *American Naturalist* 108:269-289.
- Fuentes, E.R., and P.Y. LeBoulange. 1977. The role of predation and competition in the dynamic of a grassland community in central Chile. *Terre Vie* 31:313-326.
- Fulk, G.W. 1976. Notes on the activity, reproduction, and social behavior of *Octodon degus*. *Journal of Mammalogy* 57:495-505.
- Glanz, W.E. 1982. Adaptive zones of neotropical mammals: A comparison of some temperate and tropical patterns. In M.A. Mares, and H.H. Genoways, editors. *Mammalian Biology in South America*. Special publication. Pymatuning Laboratory of Ecology, University of Pittsburgh, Linesville, Pennsylvania, USA.
- Goyal, S.P., and P.K. Ghosh. 1983. Body weight exponents of metabolic rate and minimal thermal conductance in burrowing desert rodents. *Journal of Arid Environments* 6:43-52.
- Grand, T. 1978. Adaptations of tissue and limb segments to facilitate moving and feeding in arboreal folivores. In G.G. Montgomery, editor. *The Ecology of Arboreal Folivores*. Smithsonian Institution Press, Washington, D.C., USA.
- Hart, J.S. 1957. Climatic and temperature induced changes in the energetics of homeotherms. *Revue Canadienne de Biologie* 16:133-174.
- _____. 1971. Rodents. In G.C. Whittow, editor. *Comparative Physiology of Thermoregulation*. Academic Press, New York, New York, USA.

- Hemmingsen, A.M. 1960. Energy metabolism as related to body size and respiratory structures, and its evolution. Reports of the Steno Memorial Hospital 9:1-110.
- Hennemann, W.W., III. 1983. Relationship among body mass, metabolic rate, and the intrinsic rate of natural increase in mammals. *Oecologia* (Berlin) 56:104-108.
- _____. 1984. Commentary. *Oecologia* (Berlin) 64:421-423.
- Herreid, C.F., II, and B. Kessel. 1967. Thermal conductance in birds and mammals. *Comparative Biochemistry and Physiology* 21:201-213.
- Herrington, L.P. 1940. The heat regulation of small laboratory animals at various environmental temperatures. *American Journal of Physiology* 129:123-139.
- Hershkovitz, P. 1972. The recent mammals of the neotropical region: A zoogeographic and ecological review. In A. Keast, F.C. Erk, and B. Glass, editors. *Evolution, Mammals and Southern Continents*. State University of New York, Albany, USA.
- Howe, H.F., and G.F. Estabrook. 1977. On intraspecific competition for avian dispersers in tropical trees. *American Naturalist* 111:817-832.
- Irving, L. 1951. Physiological adaptation to cold in arctic and tropical animals. *Federation Proceedings* 10:543-545.
- Irving, L., H. Krog, and M. Monson. 1955. The metabolism of some Alaskan animals in winter and summer. *Physiological Zoology* 28:173-185.
- Karami, Y., C. Rodriguez de Almeida, and F. Petter. 1976. Note sur les rongeurs du Nord-est du Bresil. *Mammalia* 40:257-266.
- Kleiber, M. 1932. Body size and metabolism. *Hilgardia* 6:315-353.
- _____. 1947. Body size and metabolic rate. *Physiological Reviews* 27:511-541.
- _____. 1961. *The fire of life*. John Wiley, New York, New York, USA.

- Kleiman, D.G., J.F. Eisenberg, and E. Maliniak. 1979. Reproductive parameters and productivity of caviomorph rodents. In J.F. Eisenberg, editor. *Vertebrate Ecology in the Northern Neotropics*. Smithsonian Institution Press, Washington, D.C., USA.
- Kliber, H.H., S. Brody, and D. Worstell. 1947. Surface area and metabolism of growing guinea pigs. *Journal of Nutrition* 33:331-338.
- Kohl, H. 1980. Temperature regulation, oxygen consumption and kidney function in the chinchilla (*Chinchilla laniger* Molina, 1782). *Zoologische Jahrbucher Physiologie* 84:472-501.
- Kulzer, E. 1973. Jugendentwicklung und temperatur-regulation beim chinchilla (*Chinchilla laniger* Molina 1782). *Zeitschrift fur Saugetierkunde* 39:231-243.
- Lacher, T.E., Jr. 1979. Rates of growth in *Kerodon rupestris* and an assessment of its potential as a domesticated food source. *Papeis Avulsos de Zoologia, Sao Paulo* 33:67-76.
- Lander, E. 1974. Observaciones preliminares sobre lapas *Agouti paca* (linne, 1966), (Rodentia, Agoutidae), en Venezuela. Universidad Central de Venezuela, Instituto de Zoologia Agricola, Maracay, Venezuela.
- Landry, S.C. 1957. The interrelationships of the New and Old World hystricomorph rodents. University of California Publications in Zoology 56:1-118.
- Lavocat, R. 1974. What is a Hystricomorph? In I.W. Rowlands, and B.J. Weir, editors. *The Biology of Hystricomorph Rodents*. Academic Press, New York, New York, USA.
- _____. 1980. The implications of rodent paleontology and biogeography to the geographical sources and origin of Platyrrhine primates. In R.L. Ciochon, and A.H. Chiarelli, editors. *Evolutionary Biology of the New World Monkeys and Continental Drift*. Plenum Press, New York, New York, USA.
- Luckett, W.P. 1980. Monophyletic or diphyletic origins of Anthropoidea and Hystricognathi: Evidence of the fetal membranes. In R.L. Ciochon, and A.H. Chiarrelli, editors. *Evolutionary Biology of the New World Monkeys and Continental Drift*. Plenum Press, New York, New York, USA.
- Mann, G.F. 1978. Los pequenos mamiferos de Chile. Gayana, Zoologia, No. 40. Ed. Univ. Concepcion, Chile.

- Mares, M.A., and R.A. Ojeda. 1982. Patterns of diversity and adaptation in South American Hystricognath rodents. In M.A. Mares and H.H. Genoways, editors. Mammalian Biology in South America. Special publication. Pymatuning Laboratory of Ecology, University of Pittsburgh, Linesville, Pennsylvania, USA.
- Mares, M.A., R.A. Ojeda, and M.P. Kosco. 1981a. Observations on the distribution and ecology of the mammals of Salta province, Argentina. *Annals of Carnegie Museum* 50:151-206.
- Mares, M.A., M. R. Willig, K.E. Streilein, and T.E. Lacher, Jr. 1981b. The mammals of Northeastern Brazil: A preliminary assessment. *Annals of Carnegie Museum* 50:81-137.
- Matamoros, Y. 1980. Contribucion al estudio de la biologia del tepezcuintle (Cuniculus paca) en cautiverio. Licenciature thesis. Universidad de Costa Rica, Costa Rica.
- McKenna, M.C. 1980. Early history and biogeography of South America's extinct land mammals. In R.L. Ciochon, and A.A. Chiarelli, editors. Evolutionary Biology of the New World Monkeys and Continental Drift. Plenum Press, New York, New York, USA.
- McNab, B.K. 1966. The metabolism of fossorial rodents: A study of convergence. *Ecology* 47:712-733.
- _____. 1969. The economics of temperature regulation in Neotropical bats. *Comparative Biochemistry and Physiology* 31:227-268.
- _____. 1970. Body weight and the energetics of temperature regulation. *Journal of Experimental Biology* 53:329-348.
- _____. 1973. The rate of metabolism of the spiny rat, Proechimys semispinosus, with comments on the ecological factors that influence the basal rate of metabolism in rodents and lagomorphs. *Boletim de Zoologia e Biologia Marinha, Sao Paulo* 30:93-103.
- _____. 1974. The energetics of endotherms. *Ohio Journal of Science* 74:370-380.
- _____. 1978a. The comparative energetics of Neotropical marsupials. *Journal of Comparative Physiology* 125:115-128.

- McNab, B.K. 1978b. Energetics of arboreal folivores: Physiological problems and ecological consequences of feeding on an ubiquitous food supply. In G.G. Montgomery, editor. *The Ecology of Arboreal Folivores*. Smithsonian Institution Press, Washington, D.C., USA.
- _____. 1979a. Climatic adaptation in the energetics of heteromyid rodents. *Comparative Biochemistry and Physiology* 62A:813-820.
- _____. 1979b. The influence of body size on the energetics and distribution of fossorial and burrowing mammals. *Ecology* 60:1010-1021.
- _____. 1980a. Food habits, energetics, and the population biology of mammals. *American Naturalist* 116:106-124.
- _____. 1980b. Energetics and the limits to a temperate distribution in armadillos. *Journal of Mammalogy* 61:606-627.
- _____. 1980c. On estimating thermal conductance in endotherms. *Physiological Zoology* 53:145-156.
- _____. 1982. The physiological ecology of South American mammals. In M.A. Mares, and H.H. Genoways, editors. *Mammalian Biology in South America*. Special publication Pymatuning Laboratory of Ecology, University of Pittsburgh, Linesville, Pennsylvania, USA.
- _____. 1983a. Energetics, body size, and the limits to endothermy. *Journal of Zoology, London* 199:1-29.
- _____. 1983b. Ecological and behavioral consequences of adaptation to various food resources. In J.F. Eisenberg and D.G. Kleiman, editors. *Advances in the Study of Mammalian Behavior*. American Society of Mammalogists, Special Publication No. 7.
- _____. 1984. Physiological convergence amongst ant-eating and termite-eating mammals. *Journal of Zoology, London* 203:485-510.
- _____. 1985. The influence of food habits on the energetics of Eutherian mammals. *Ecology*. In press.
- McNab, B.K., and W. Auffenberg. 1976. The effect of large body size on the temperature regulation of the komodo dragon, *Varanus komodoensis*. *Comparative Biochemistry and Physiology* 55A:345-350.

- McNab, B.K., and P.R. Morrison. 1963. Body temperature and metabolism in subspecies of *Peromyscus* from arid and mesic environments. *Ecological Monographs* 33:63-82.
- Meserve, P.L. 1981. Resource partitioning in a Chilean semi-arid small mammal community. *Journal of Animal Ecology* 50:745-757.
- Morris, D. 1962. The behaviour of the green acouchi (*Myoprocta pratti*) with special reference to scatter hoarding. *Proceedings of the Zoological Society of London* 139:701-733.
- Morrison, P.R., and F.A. Ryser. 1951. Temperature and metabolism in some Wisconsin mammals. *Federation Proceedings* 10:93-94.
- _____. 1952. Weight and body temperature in mammals. *Science* 116:231-232.
- Morton, E.S. 1973. On the evolutionary advantages and disadvantages of fruit eating in tropical birds. *American Naturalist* 107:8-22.
- Nowak, R.M., and J.L. Paradiso. 1983. *Walker's mammals of the world*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Ojasti, J. 1972. Revision preliminar de los picures o agouties de Venezuela (Rodentia, Dasyproctidae). *Memorias de la Sociedad de Ciencias Naturales La Salle* 32:159-204.
- Orsetti, R.F., and J.J. McNamus. 1971. Temperature regulation in the chinchilla, *Chinchilla laniger*. *Bulletin New Jersey Academy of Science* 16:27-29.
- Palacio, C. 1977. Standard metabolism and thermoregulation in three species of lorosoid primates. Dissertation. University of Florida, Gainesville, Florida, USA.
- Parra, R. 1978. Comparison of foregut and hindgut fermentation in herbivores. In G.G. Montgomery, editor. *The Ecology of Arboreal Folivores*. Smithsonian Institution Press. Washington, D.C., USA.
- Patterson, B., and R. Pascual. 1972. The fossil mammal fauna of South America. In A. Keast, F.C. Erk, and B. Glass, editors. *Evolution, Mammals and Southern Continents*. State University of New York, Albany, USA.
- Payne, P.R., and E.F. Wheeler. 1968. Comparative nutrition in pregnancy and lactation. *Proceedings of the Nutrition Society's* 27: 27: 129-138.

- Pianka, E.R. 1978. *Evolutionary Ecology*. Harper and Row, New York, New York, USA.
- Roberts, C.M., and J.S. Perry. 1974. Hystricomorph embryology. In I.W. Rolands and B. Weir, editors. *The Biology of Hystricomorph Rodents*. Academic Press, New York, New York, USA.
- Rosenmann, M.A. 1977. Regulacion termica en Octodon degus. Medio Ambiente (Chile) 3:127-131.
- Sarich, V.M., and J.E. Cronin. 1980. South American mammal molecular systematics, evolutionary clocks, and continental drift. In R.L. Ciochon and A.B. Chiarelli, editors. *Evolutionary Biology of the New World Monkeys and Continental Drift*. Plenum Press, New York, New York.
- Scholander, P.F., R. Hock, V. Walters, and L. Irving. 1950a. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. *Biological Bulletin* 99:259-271.
- Scholander, P.F., R. Hock, V. Walters, F. Johnson, and L. Irving. 1950b. Heat regulation in some arctic and tropical mammals and birds. *Biological Bulletin* 99:237-258.
- Scholander, P.F., V. Walters, R. Hock, and L. Irving. 1950c. Body insulation of some arctic and tropical mammals and birds. *Biological Bulletin* 99:225-236.
- Segal, A.N. 1978. Thermoregulation in Myocastor coypus in summer. *Zoologicheskii Zhurnal* 57:1878-1883.
- Simonetti, J.A., and G. Montenegro. 1981. Food preferences by Octodon degus (Rodentia:Caviomorpha): their role in the Chilean matorral composition. *Oecologia* (Berlin) 51:189-190.
- Simpson, G.G. 1980. *Splendid Isolation. The Curious History of South American Mammals*. Yale University Press, New Haven, Connecticut, USA.
- Smythe, N. 1970. Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. *The American Naturalist* 104:25-35.
- _____. 1978. The natural history of the Central American agouti (Dasypsecta punctata). *Smithsonian Contributions to Zoology* 157:1-52.

- Smythe, N., W.E. Glanz, and E.G. Leigh, Jr. 1982. Population regulation in some terrestrial frugivores. In E.G. Leigh, Jr., A.S. Rand and D.M. Windsor, editors. The Ecology of a Tropical Forest. Smithsonian Institution Press, Washington D.C., USA.
- Snow, D.W. 1962. The natural history of the oilbird (Steatornis caripensis) in Trinidad, W.I. II. Population, breeding ecology and food. Zoologica 47:199-221.
- Sokal, R.R., and F.J. Rohlf. 1969. Biometry. Freeman, San Francisco, California, USA.
- Stern, J.J., and A. Merari. 1969. The bathing behavior of the chinchilla. Psychonomic Science 14:115.
- Streilein, K.E. 1983a. The ecology of small mammals in the semiarid Brazilian Caatinga. I. Climate and faunal composition. Annals of the Carnegie Museum 51:79-107.
- _____. 1982b. The ecology of small mammals in the semiarid Brazilian Caatinga. II. Water relations. Annals of the Carnegie Museum 51:109-126.
- _____. 1982c. The ecology of small mammals in the semiarid Brazilian Caatinga. IV. Habitat selection. Annals of Carnegie Museum 51:331-343.
- Verner, K.J., V.C. Wells, III, T.J. Puggard, T.J. Sloan, and M. Bannow. 1980. The effect of circadian cycle on the sensitivity to thermal load in the chinchilla. Comparative Biochemistry and Physiology 66A:149-151.
- Webb, S.D., and L. G. Marshall. 1982. Historical biogeography of recent South American land mammals. In M.A. Mares, and H.H. Genoways, editors. Mammalian Biology in South America. Special publication Pymatuning Laboratory of Ecology, University of Pittsburgh, Linesville, Pennsylvania, USA.
- Weir, B. 1974. Reproductive characteristics of Hystricomorph Rodents. In I.W. Rowlands and B. Weir, editors. The Biology of Hystricomorph Rodents. Academic Press, New York, New York, USA.
- Wilcox, H.H. 1950. Histology of the skin and hair of the adult chinchilla. Anatomical Record 108(3):385-397.
- Wood, A.E. 1974. The evolution of the Old World and the New World hystricomorph. In I.W. Rowlands and B. Weir, editors. The Biology of Hystricomorph Rodents. Academic Press, New York, New York, USA.

- Wood, A.E. 1980. The origin of the caviomorph rodents from a source in Middle America: A clue to the area of origin of the Platyrrhine primates. In R.L. Ciochon, and A.H. Chiarelli, editors. Evolutionary Biology of the New World Monkeys and Continental Drift. Plenum Press, New York, New York, USA.
- Woods, C.A. 1982. The history and classification of South American hystricognath rodents--reflections on the far away and long ago. In M.A. Mares and H.H. Genoways, editors. Mammalian Biology in South America. Special publication Pymatuning Laboratory of Ecology, University of Pittsburgh, Linesville, Pennsylvania, USA.
- _____. 1984. Hystricognath rodents. In S. Anderson and J.K. Jones, Jr., editors. Orders and Families of Recent Mammals of the World. J. Wiley and Son, Inc., New York, New York, USA.
- Woods, C.A., and D. Boraker. 1975. Octodon degus. Mammalian Species. 67:1-5.
- Zeinert, K. 1983. Husbandry of chinchillas. Veterinary Medicine 78:1292-1294.
- Zullinger, E.M., R.E. Ricklefs, K.H. Redford, and G.M. Mace. 1984. Fitting Sigmoidal equations to mammalian growth curves. Journal of Mammalogy 65:602-636.

BIOGRAPHICAL SKETCH

Alexis Arends Rodriguez was born on October 22, 1948 in Caracas, Venezuela. He attended the Facultad de Ciencias, Universidad Central de Venezuela, where he received a degree of Licenciatura en Biologia in 1974. Mr. Arends entered graduate school at the University of Florida in 1975 to pursue a Ph.D. in Zoology. His main research interest was physiological ecology of mammals. During his graduate studies, Mr. Arends was supported by a scholarship from the Universidad Central de Venezuela.

In 1980, he began working as an assistant professor at the Universidad Nacional Experimental Francisco de Miranda in Coro, Venezuela. In 1982, he was promoted to aggregate professor. After receiving his Ph.D. in May 1985, Mr. Arends will continue working there, at the Centro de Investigaciones en Ecologia y Zonas Aridas.

Since June 1974, Mr. Arends has been married to the former Miriam L. Diaz Pino and they have two sons, Tulio Francisco and Alberto Jose.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



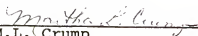
B.K. McNab, Chairman
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



F.G. Nordlie
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



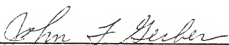
M.L. Crump
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



J.F. Anderson
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



J.F. Gerber
Professor of Fruit Crops

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy

May, 1985

Dean for Graduate Studies and
Research